# IMPACTS OF LAND USE ON THE RIPARIAN FOREST ALONG THE ASSINIBOINE RIVER.

By

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A thesis
submitted to the Faculty of Graduate Studies
of the University of Manitoba
in partial fulfillment of the requirements for the degree of
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# ABSTRACT

Extensive landscape modification from surrounding land use has led to the decline of riparian forests across North America. An urban – rural gradient was used to assess the impact of land use on riparian forests along the Assiniboine River. Above ground flora and seed bank were examined and species- and guild-level indicators of disturbance identified. Twenty-five sites were categorized according to land use, and included urban, suburban, high intensity rural, low intensity rural, and relatively high quality reference forests. Changes in herbaceous, shrub, and tree species composition and diversity were related to landscape level measures of disturbance that included the proportion of surrounding land use, forest patch size, connectivity, and area:perimeter ratio.

Urban forests were highly fragmented and the most adversely affected by surrounding land use. They were small, isolated, lacked interior, and characterized by relatively dry and alkaline soils. They had the lowest native and overall understorey and seed bank species diversity, highest proportion of exotic species, and the lowest seed density. Indicators of disturbance, typically opportunistic species, were significantly more common in these urban forests and included *Solanum dulcamara, Rhamnus cathartica*, and *Lonicera tartarica*. Suburban forests were less disturbed, but had been recently subjected to extensive development-related clearing and fragmentation. Although reference sites were relatively large and exhibited greater connectivity, there was little difference in species composition among low and high intensity rural and reference sites. Indicators of high integrity forest, typically vulnerable species, were significantly more frequent in these non-city land use types, and included *Rubus idaeus, Carex* spp., and *Galium triflorum*.

Generalists dominated (69 %) the understorey community, whereas opportunistic (15 %) and vulnerable (16 %) species were relatively less common. Opportunistic species tended to be exotic, woody and annual, and effective dispersers (i.e. endozoochores). In contrast, vulnerable species tended to be native, perennial, and ineffective dispersers (i.e. barichores or anemochores). In total 197 taxa were identified in the above ground flora, compared to 90 taxa in the seed bank. Of the latter, the three most frequent species, *Poa pratensis*, *Sonchus arvensis*, and *Cirsium arvense*, were all exotic.

These results suggest that landscape measures of disturbance, and related changes in environment, may be confidently used to assess the impacts of land use along urban-rural gradients. Changes in seed bank of this important riparian forest system suggest that the current decline will continue especially if future forest regeneration is solely dependent upon the seed bank. Opportunistic and vulnerable species, and their associated guilds can be used as effective indicators of disturbance and forest integrity and be used to select and monitor forests for further protection or active management.

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# CHAPTER 1: General Introduction

Riparian habitat represents an important ecotone between aquatic and terrestrial ecosystems. The riparian forest plays an important role in the structure and function of rivers (Brinson & Ver Hoeven 1999). Their numerous ecological benefits include stabilizing river banks (Malanson 1993), reducing erosion, absorbing nutrient and pesticide runoff (Karr & Schlosser 1978), protecting aquatic habitat and water quality (Delong & Brusven 1998), acting as corridors for species dispersal, and providing habitat for many animal and plant species (Cordes et al. 1997). Additionally, they provide human benefits, as, in urban environments they are often the only natural green space remaining for human health and enjoyment (Airola & Buchholz 1984). Despite the importance of these forests, they are in decline due to anthropogenic disturbance, and are now recognized across North America as an endangered ecosystem (Knutson & Klaas 1998).

In North America, past agricultural and ongoing urban conversion of natural habitat is leading to extensive landscape modification. Riparian forests are being fragmented, resulting in both habitat loss and the degradation of remnant habitat. The serpentine nature of riparian forests, having lots of edge, makes them especially susceptible to disturbance (Planty-Tabacchi et al. 1996). As anthropogenic disturbance increases, remnant patches are decreasing in size, in turn consisting of more edge habitat and becoming more isolated (Davis & Glick 1978). These landscape-level changes are thereafter associated with abiotic and biotic site level changes.

This disturbance is not going unnoticed. There is increasing interest by landowners, community groups, and the municipal government in protecting remnant riparian forest. The city of Winnipeg currently has a system, using the abundance of exotic and ruderal species, for ranking the quality of riparian forest patches. Many community groups have used this system to assess areas of interest, in particular along the LaSalle River. Additionally, the city manages some of these forests by fencing off areas to allow them to regenerate. As a test area, for example, a 50 x 20 m patch in Assiniboine Park was fenced off for a couple of years. Outside of Winnipeg, many landowners display a strong interest in preserving their extant riparian forest, some of which are already actively managed by these landowmders for Dutch Elm disease. Despite this interest and concern there is very little information regarding the impacts of disturbance. The overall objective of this study was to identify effects of land use along an urban-rural gradient on the Assiniboine River riparian forest, in Southwestern Manitoba, Canada. Chapter objectives and specific questions addressed are as follows;

## LIST OF OBJECTIVES

Objective one: To assess the impact of surrounding land use on the aboveground flora of fragmented riparian forests along the Assiniboine River (Chapter 3). In particular,

- What changes in plant community species composition and diversity occur in response to the different types of land use?
- What is the relative importance of the disturbance and environment variables in determining plant community species composition?
- How does the land use gradient affect the edge-to-interior gradient within extant forest?

Objective two: To describe the seed bank of riparian forests along the Assiniboine River and its response to surrounding land use (Chapter 4). In particular,

- What is the species composition and diversity of the riparian forest seed bank, and how are they affected by disturbance and environmental variation?
- How are species composition and diversity of the seed bank affected by surrounding land use?

Objective three: To identify effective indicators of riparian forest degradation associated with land use (Chapter 5). In particular I wanted to

- Identify species that exhibited significant relationships with changes in environment and disturbance associated with land use.
- Identify guild-level characteristics that underlay species-level response to land use.
- Identify species that were good indicators of changes in species diversity associated with land use.

# CHAPTER 2: Literature Review

## INTRODUCTION

With the ever-increasing human population and associated urban expansion, landscapes are undergoing extensive modification, leading to widespread habitat fragmentation. Fragmentation has been described as the greatest threat to and cause of species extinction (Wilcox & Murphy 1985). For birds and mammals there is an approximate threshold of 10 – 30 % useable remnant habitat in the landscape required to maintain biodiversity (Andrén 1994). The sixth great extinction event is thought to be currently occurring, as 0.5 % of species worldwide become extinct per year (Woodwell 1990; Wilson 1992), and biodiversity concerns have become a global issue. Additionally, conservation of urban ecosystems is becoming paramount, in light of the increased urbanization (McDonnell & Pickett 1990). Of particular concern to this study, approximately 75% of riparian habitat in Winnipeg has been disturbed or cleared by urban development (C. Heming pers. comm.). It is important, therefore, to study the effects and disturbance from human land use, in an attempt to protect or restore habitat and slow the rate of habitat fragmentation and species loss.

## FRAGMENTATION

Fragmentation refers to the division of contiguous areas of native vegetation into smaller remnants or habitat islands separated by a matrix of contrasting human land use (Saunders et al. 1991). Although forested landscapes in North America were originally fragmented by agricultural use, urban expansion now increasingly fragments extant natural habitat. The degree of forest fragmentation, at a landscape scale, can be predicted by human population density (Vogelmann 1995). Although research on forest fragmentation was initially influenced by the equilibrium theory of island biogeography (MacArthur & Wilson 1967) it is increasingly influenced by metapopulation theory (Levins 1970). Fragmentation affects patch size, shape, and connectivity and is characterized by habitat loss and the associated increased proportion of edge habitat and isolation of remnant habitat (Godron & Formann 1983). The severity of these effects increases above a threshold of approximately 20 % anthropogenic land use cover (Vogelmann 1995; Wickham et al. 1999).

### Habitat Loss

Habitat loss refers specifically to the elimination of habitat, associated with conversion of natural habitat, the isolation of remnant habitat, and the deterioration of habitat within and among remnant patches (Sih et al. 2000). The loss and degradation of habitat increase extinction rates, and the reduction in quality of surrounding land, decreases rates of recolonization. Over time, habitat loss leads to progressively smaller forest patches and is often associated with reductions in plant species diversity (e.g., Airola & Buchholz 1984; Vogelmann 1995). At the original time of fragmentation, there may be an initial increase in species diversity, either from transient species using remnants as habitat refugia or from early-successional species introduced from the surrounding matrix (Debinski and Holt 2000). However, many species will later be lost through species interactions (Sih et al. 2000) or as a result of area reduction through species relaxation (Saunders et al. 1991). The smaller a remnant becomes, the more likely it is influenced by external factors such as edge effects (Saunders et al. 1991). Habitat loss is thought to be one of the greatest causes of species decline, and may contribute to the loss of 50 % of the earth's species within the next 50 years (Sih et al. 2000).

### Edge Effects

Edge effects occur when there is an abrupt change from one ecosystem to another, and lead to changes in both abiotic and biotic conditions at the interface (Murcia 1995). For forests, three general types of edges are differentiated according to the location of initial edge formation relative to the location of edge maintenance: cantilevered, canopy dripline, and advancing (Ranney et al. 1981). Cantilevered edges are maintained at the base of the trees where the edge was initially formed, and overhang the adjacent land use. In contrast, canopy dripline and advancing edges are not maintained at the point of initial edge formation. Canopy dripline edges are maintained at the outer branch limit of canopy trees, and have a dense understorey of herbs and shrubs. Advancing edges are maintained beyond the tree dripline into the adjacent land use, and have dense vegetation that declines in height from the created to the maintained edge.

Forest edges tend to be associated with increases in radiation fluxes, temperature, wind, and declines in relative humidity and soil moisture (Saunders et al. 1991; Brothers & Spingarn 1992; Murcia 1995; Burke & Nol 1998). Replacement of native vegetation, often having complex vertical structure, with cultivated species, tends to increase the exposed ground surface. Radiation balance is altered by changing the albedo, with increased insolation during the day and re-radiation during the night (Saunders et al. 1991; Brothers & Spingarn 1992). These changes lead to higher daytime and lower nighttime air temperatures, which in turn, lead to higher soil temperatures (Saunders et al. 1991; Brothers & Spingarn 1992; Burke & Nol 1998). Altered landscape structure also affects the natural wind patterns that a species would normally be subject to and increases the wind speed (Saunders et al. 1991). Trees maturing in a closed canopy lack the support mechanism necessary to protect them against strong winds on fragmented edges, thus subjecting them to greater damage from windthrow or pruning (Chen et al. 1992). This increased damage, in turn, creates more canopy openings along the edge (Saunders et al. 1991; Fraver 1994). Increased wind exposure may increase evapotranspiration, which in combination with the higher temperatures and altered rainfall interception from the removal of the native vegetation ultimately changes soil moisture levels (Saunders et al. 1991). Thus, edges of fragmented forests in Eastern Canada were found to have lower soil moisture relative to the forest interior (Burke & Nol 1998).

Changes in the microenvironment of forest edges results in different species composition and structure compared to forest interiors. If these changes modify features beyond their historical range of variation, then the changes can be long lasting as the altered edge is no longer suitable for the original ecosystem (Murcia 1995). In general, forest edges are more susceptible to establishment by xeric, early successional, and shade intolerant species as well as invasion by exotic species (Brothers & Spingarn 1992; Fraver 1994). Although impacts of edges on shrub and tree layers have received much attention, impacts on the understorey herbaceous layer have largely been overlooked (Burke & Nol 1998).

Changes to the edge shrub and tree layers associated with edge conditions include increases in basal area and stem density (Ranney et al. 1981; Chen et al. 1992; Burke & Nol 1998), tree mortality (Chen et al. 1992), and species richness (Ranney et al. 1981; Brothers & Spingarn 1992). In turn, changes in the herbaceous layer include lower densities or absence of some understorey forest species (Ranney et al. 1981; Chen et al. 1992; Burke & Nol 1998), increased densities of edge-associated species, which may be restricted to edge habitat (Ranney et al. 1981; Chen et al. 1992; Fraver 1994), increased species richness (Burke & Nol 1998), and increases in the number of exotic or invasive species (Ranney et al. 1981; Brothers & Spingarn 1992; Fraver 1994).

Although edge effects are understood, there is often little consistency in generalizable results among studies, this arising from poor design, inconsistent methodology, and the over simplification of edge effects (Murcia 1995). Poor design arises from a lack of replication or use of pseudo-replication, often associated with studies of the natural environment, which can lead to confounding effects. Inconsistency in studies of edge effects arises from a poor description of the surrounding area or a failure to differentiate among edge types. Despite these inconsistencies, few studies show changes in native species composition and interior conditions that extend 20m beyond the forest edge (Murcia 1995; Burke & Nol 1998).

Changes in environmental conditions and vegetation response are considerably influenced by the different physiognomy of the three edge types (Ranney et al. 1981; Murcia 1995). The guarded and more intact structure of an advancing edge not only will reduce changes in the environmental conditions, but functions as a barrier, thus reducing the number of wind dispersed exotic species that reach the forest interior from the surrounding landscape (Cadenasso & Pickett 2001). Intensity of edge effects also varies in response to orientation, with the greatest effects in the Northern Hemisphere typically on south or west facing edges (Palik & Murphy 1990; Saunders et al. 1991). Additionally, the relative proportion of area that is edge habitat increases, as a remnant forest patch becomes smaller. For example, Fraver (1994) suggested that a 1000 ha square forest would be only 5 % edge habitat, whereas 100, 10, and 1 ha square forest remnants would be 14 %, 42 %, and 94 % edge, respectively. Core area of a remnant patch declines sharply with patch size, but this rate is also dependent on shape (Laurance & Yensen 1991). Any linear remnant patch with a width less than 30 m would be entirely dominated by edge having no effective interior, regardless of size (Ranney et al 1981). To conserve any interior habitat Matlack (1994a) proposed a minimum patch size of 0.5 ha for a circular reserve, although a minimum of 2.7 ha would be required to also protect interior habitat from central disturbances such as treefall gaps.

### Isolation

As landscapes become fragmented, distances generally increase among remnant patches and any connecting corridors tend to be eroded (Brothers & Spingarn 1992). Between the aforementioned 20 % threshold and 40 % anthropogenic land-use cover there is still potential to increase connectivity; however, once human use is greater than 40 % of the landscape remnant forest patches tend to be too small and isolated (Wickham et al. 1999). Distance among patches and their connectivity have important implications for colonization and plant distributions in relation to seed dispersal (Primack & Miao 1992). As isolation increases, dispersal-restricted species such as ant-, gravity-, explosive-, and wind-dispersed species with heavy seeds may become extirpated (Dzwonko & Loster 1992). For example, the recruitment rate and population size of *Trillium* was reduced by isolation (Jules 1998). Animal dispersed species that are generally not dispersal-restricted may also be affected by isolation when the disperser is adversely affected by the surrounding matrix (Grashof-Bokdam 1997). Many early successional, and exotic, plant species, however, are effective dispersers under these conditions (Stylinski & Allen 1999).

### Land Use

Over the last three hundred years, landscapes across North America have become fragmented by agricultural use. There has been a consequent shift in land use from prairies and late-successional forests dominated by perennial species to relatively homogenous landscapes that are dominated by annual crop and weed species (Delong & Brusven 1998). These agricultural systems are generally intensively managed and require substantial nutrient and pesticide inputs (Lowrance et al. 1984). Additionally, maintained edges have relatively greater impacts than more temporary edges associated with other types of land use disturbances such as logging (Fraver 1994).

More recently, a shift in the economic base from one dependent on agriculture to one that includes industry and service (Dickinson 1966) has led to urban expansion and an associated conversion of cropland and natural habitat into urban land use (McDonnell & Pickett 1990). Globally, the human population is growing at a rate of 1.8 % per year. In industrialized nations approximately 75 % of the population lives in cities, and in developing countries urban centers are the loci of population growth (Matson 1990). This urban expansion leads to further decreases in patch size within cities and an increased isolation from other urban and rural remnant patches (Davis & Glick 1978). This extensive landscape modification has lead to a complex urban-rural gradient which, as an extension of Robert Whittaker's (1967) gradient paradigm, represents an important tool that can be used to address ecological questions at the landscape level of organization (Matson 1990; McDonnell et al. 1993).

Landscape ecology and the application of urban-rural gradients is a new area of study in which many of the questions are exploratory (McDonnell & Pickett 1990). Of particular interest is how patch size, shape, and isolation relate to the land use gradient and how these changes affect species composition and underlying processes including seed dispersal. Urban-rural gradient studies show that urban land use is associated with a decline in forest species diversity (Airola & Buchholz 1984) and native understorey species (Hoehne 1981; Cole & Marion 1988; Kuss & Hall 1991; Robinson et al. 1994), and an increase in exotic and ruderal species diversity (Hoehne 1981; Rudnicky & McDonnell 1989; Robinson et al. 1994; Freedman et al. 1996). In addition to the biotic response, urban land use is associated with higher pollution levels, more heavy metals in the soil, and hydrophobic soils (McDonnell et al. 1993). Typically, extant urban forest is severely disturbed, especially by human trampling (Hoehne 1981; Rudnicky & McDonnell 1989; Matlack 1997a) that results in removal of leaf litter and soil compaction (Rudnicky & McDonnell 1989). Species diversity and tree density and basal area in forests were found to be positively associated with patch size and connectivity and negatively associated with pollution and human impacts (Airola & Buchholz 1984). Whereas the urban – rural gradient has also been used in studies of tree ring chemistry (Watmough et al. 1998), wildlife (Limburg & Schmidt 1990; Bowers & Breland 1996; Clergeau et al. 1998), water quality (Wear et al. 1998), and heavy metal accumulation in soils (Pouyat & McDonnell 1991), to my knowledge it has not been applied to the study of riparian forests.

## LANDSCAPES

### Island Biogeography

The impacts of forest fragmentation were initially related to MacArthur and Wilson's (1967) theory of island biogeography. This was one of the first models of species diversity and population dynamics, and examined the ability of species to colonize and persist on offshore islands. It postulated that species richness is in a dynamic equilibrium maintained by the immigration and extinction of species, whereby more distant islands are relatively slowly colonized by new species, and smaller islands experience greater species extinction in response to demographic and genetic stochasticity (Hanski & Simberloff 1997).

The immigration rate of an unpopulated island will be high, as colonizing species are new to that island. However, as the number of resident species increases the number of new species declines causing a lower immigration rate (Begon et al. 1996). Once all the species from the 'source pool' (i.e. from surrounding islands or mainland) are represented, then the immigration rate to the island of interest reaches zero. The rate of immigration is affected by an island's remoteness, as colonizers will likely have a greater chance of reaching islands closer to the 'source pool'. Additionally, the rate of immigration is affected by island size and will likely be higher for larger islands, as they represent a larger 'target' for colonizing species (Begon et al. 1996).

The extinction rate on an unpopulated island will be zero, as there are no species to become extinct (Begon et al. 1996). When there are few resident species the extinction rate will be low. However, as the number of resident species increases, the rate of extinction quickly increases, due to both increased competitive exclusion and smaller population sizes for each species, which are more vulnerable to chance extinction. The rate of extinction is affected by island size, as smaller islands typically have smaller populations, shown by species-area relations, thus making them more susceptible to chance extinction.

The dynamic equilibrium of species richness is located at the intersection of the immigration and extinction rate curves. This was empirically shown in a study of very small "island" patches in Florida where recolonization rates from the mainland were monitored following invertebrate removal using a pesticide treatment (Simberloff & Wilson 1969). Although the theory of island biogeography was developed for real terrestrial islands in a non-terrestrial matrix, it has since been applied to terrestrial landscapes. Fragmented forest patches were viewed as forest "islands" in a sea of agriculture and urban land use (Davis & Glick 1978; Burgess & Sharpe 1981). By the mid 1970s, this theory dominated conservation biology and was the guiding factor behind the development of "rules" for refuge design (Hanski & Simberloff 1997).

The comparison and application of island biogeography to remnant forests in human dominated landscapes has several problems. Remnant forests are not true islands in the sense that the surrounding landscape is not entirely alien and impenetrable to terrestrial biota (Burgess & Sharpe 1981). Indeed, some terrestrial species actually favour these disturbed landscapes. This view reflects the preoccupation of conservation biologists with natural habitat and their relative collective ignorance of resource management systems such as agriculture and forestry (S. McLachlan pers. comm.). The relative ability of a species to colonize these forest islands depends on the species characteristics in relation to the structure of the surrounding landscape affected by land use. Additionally, the theory of island biogeography assumes only immigration from mainland to the island whereas, with remnant forests there is also interaction between the forest islands and surrounding matrix. Remnant urban forests, as habitat islands, are dominated by aggressive ruderal species that have been introduced from the surrounding matrix (Davis & Glick 1978). There was a shift in emphasis among conservation biologists in the late 1980s, from island biogeography to metapopulation theory (Levins 1969, 1970; Hanski & Simberloff 1997).

### Metapopulation Theory

The general description of metapopulations is a group or population of discrete local populations having species turnover within and migration among these local populations (Begon et al. 1996; Hanski & Gilpin1997). The term 'meta' is used, as the linkage among the local populations increases the ability of the larger regional population to survive (Begon et al. 1996). The persistence of a metapopulation is affected both by repeated extinction of occupied patches and recolonization of unoccupied patches (Hooftman et al. 1999; Sih et al. 2000). As a result of differing spatial population structures, several variations to the general description have developed and include: Levins classical metapopulations, source-sink metapopulations, and nonequilibrium metapopulations (Hanski 1996; Hanski & Simberloff 1997).

Levins classical metapopulation theory was initiated as a simple population ecology model to assess population persistence using colonization and extinction parameters (Hanski 1996; Hanski 1997). It assumes that space is discrete, in other words, one can distinguish between habitat patches and the surrounding matrix (Hanski & Simberloff 1997). Following this assumption, MacArthur and Wilson's (1967) theory of island biogeography can be seen as a multi-species and island-mainland representation of Levins model (Hanski 1996). Three other assumptions of an ideal metapopulation are that: 1) habitat patches are equal in size and isolation, 2) local populations are discrete having independent dynamics, and 3) migration rates among local population is low enough to not effect local dynamics of existing populations (Hanski & Simberloff 1997).

Several of the classical metapopulation assumptions are not met however, in landscape ecology studies of habitat fragmentation. The classical view of distinct patches in a featureless matrix ignores the reality of surrounding land use forming a complex mosaic of other patches, corridors, and barriers (Wiens 1997). This complex matrix will alter an individuals dispersal ability, thus impeding patch recolonization (Wilcox & Murphy 1985; Sih et al. 2000). The different surrounding land uses likely will also undermine the assumption of equal size and isolation of remnant habitat. Additionally, the classical metapopulation theory was developed for animals and is less applicable to the study of plants (Hooftman et al. 1999). Early empirical support of classical metapopulation was conducted with butterfly (Thomas & Hanski 1997) and amphibian (Harrison & Taylor 1997) populations. Plants, in comparison, are more resistant to extinction, having relatively longer life spans and persistent propagule banks. In turn, their relatively restricted dispersal and often sporadic recruitment reduces their recolonization ability (Hooftman et al. 1999). Thus, plant populations are more appropriately related to the source-sink metapopulation model. Here, there are high quality habitat patches where the population growth rate is positive and acts as a source for immigration to low quality habitat patches, thus preventing local extinction from a negative population growth rate (Begon et al. 1996; Hanski & Simberloff 1997).

Problems arise when metapopulation is broadly applied without empirical support. Not all species fit into metapopulation dynamics, and theoretically classical metapopulation focuses on single species, and is unable to reflect entire communities (Harrison & Taylor 1997). Additionally, metapopulation assumes homogenous remnant patches, ignoring the effects of different patch quality. Studies of human-fragmented landscapes have found patches of different quality that display non-equilibrium situations, with divided populations that exhibited local extinction and did not form a functional metapopulation (Hanski & Simberloff 1997). Finally, the rate of fragmentation is now so fast that the environment may change faster than the extinction-colonization equilibrium of metapopulation can be reached, leading to a non-equilibrium decline of the population (Hanski 1996). Despite these problems metapopulation theory continues to dominate conservation biology as island biogeography had in the 1970s (Hanski & Simberloff 1997).

## ECOSYSTEMS

Vegetation change is universal as species are introduced or become extinct in response to environmental conditions, and in turn changing the conditions. Vegetation composition of an area results from the selection of species arriving in the seed rain and immigration, in response to temporally and spatially changing environmental conditions. Patches that have developed under similar conditions were found to have recognizable vegetation 'types', and led to the concept of plant communities, which Clements (1916) considered as analogous to a complex organism (Miles 1982; McCook 1994). These systems display emergent properties of structural organization, species diversity, and vegetation stability, not characteristic of their individual species.

A distinction is made in vegetation change between fluctuations, whereby changes are short term and reversible and succession, whereby changes are directional and continuous, with the vegetation composition changing to a different and recognizable community (Miles 1982; Begon et al. 1996). Succession can be divided into primary and secondary processes, whereby primary succession is the colonization of previously un-vegetated areas, following glacial receding or volcanic eruptions, for example. In comparison, this discussion focuses on secondary succession, whereby an area is re-vegetated after a severe disturbance has removed existing vegetation but in which a well developed soil and seed bank remain intact (Miles 1982; Begon et al. 1996).

Succession theory began to be developed in the late 1800s, with the basic architecture of the theory worked out between 1859 – 1900 (Johnson 1979). In this period, Cowles (1899) was the first to fully describe the sequence of forest succession. The period between 1900 – 1930 was dominated by the work of Clements (1916, 1928, 1936), whose model of succession was so comprehensive that the concept remains associated with his thinking (Miles 1982). His idea of succession was of directional change, with one vegetation type modifying the site to favour the successive vegetation type (McCook 1994). This replacement continued, until a stable and self-maintaining climax vegetation type was reached, with the exact process replicated again if the climax community was lost due to a catastrophic event (Miles 1982). The third period of successional theory development occurred between 1930-1947, in which Gleasonian views were favoured (Johnson 1979). Gleason (1926) had an 'individualistic' concept and argued that a community's properties were dependent on the properties of the individual species composing it (Miles 1982).

A major criticism of the successional concepts by both Clements and Gleason was that they considered disturbance to be non-essential and uncommon in the process of succession (Cook 1996). Another criticism of Clements' classical model, is that neither the composition of vegetation, nor the seed bank, would be precisely the same for any two patches, and thus, succession of the patches would proceed differently (Miles 1982). A further criticism is that Clements overemphasized the importance of facilitative changes in establishing later successional species, as most of the species are often already present as seeds or propagules at the outset of succession but are subject to different growth and reproduction rates (Miles 1982). Following these criticisms less emphasis was put on the classical succession model, which led, post-1949, to the development of 'modern' theory (Johnson 1979).

Drury and Nisbet (1973) proposed that the theory of succession be developed based on the different physiological and ecological tolerances of species in different environments (Miles 1982; Cook 1996). Realizing the great complexity and variation in vegetation and that most vegetation around the world is in a state of change responding to natural disturbance, there is not a single all-embracing succession model (Miles 1982). Despite this, the main views on succession exhibit several common themes. Disturbance and random factors influence vegetation dynamics and operate at various spatial and temporal scales. As such, various mechanisms, and sometimes more than one at a time, drive succession with many systems not even reaching a stable climax state (Cook 1996). Additionally, the attributes and life histories of the individual species are important in determining the succession of the community.

Three general models of succession are facilitation, tolerance, and inhibition, which incorporate differences in species establishment, competitiveness, and longevity (Cook 1996). Facilitation is essentially the Clements model, where early colonizers alter the environment to favour the establishment of later successional species; however, clear-cut stages are rarely found (Miles 1982). In the tolerance model successional changes are mediated by species characteristics, such as life history, dispersal mechanism, and efficiency of resource use (Cook 1996). This follows Egler's (1954) initial floristic composition factor whereby all species are present from the outset of succession but in which different growth rates, reproductive rates, and life span determine successional changes in species dominance (Miles 1982). The inhibition model is the opposite of facilitation, as any population along the successional sequence may inhibit the invasion of other species temporarily impeding succession (Cook 1996). Inhibition occurs through a variety of ways but the most common is physical occupancy, which monopolizes light resources, until the inhibiting species is damaged or dies (Miles 1982).

The change of focus to species level succession required a better understanding and description of species response. Two very contrasting species-level responses were called r- and k-strategists (MacArthur & Wilson 1967). R-strategists are colonizers that are typically fast-growing, shade intolerant, and short lived herbs, that produce a large number of small and long lived seeds that are effectively dispersed and persistent in the seed bank (Miles 1982; Begon et al. 1996). K-strategists, in comparison, are slow-growing, shade tolerant, and long lived trees, that produce relatively fewer, larger, and shorter lived seeds that are poorly dispersed and not persistent in the seed bank. R- and k-strategists are relative terms but distinctly r-strategists species were referred to as 'early-successional' species, whereas k-strategists were traditionally referred to as 'climax' or 'late-successional' species (Miles 1982). Grime (1977) expanded on this idea and further categorized herbaceous species according to stress, disturbance, and competition related strategies (Miles 1982; Begon et al. 1996). When stress, a shortage of resources, was high and disturbance uncommon then a 'stress-tolerant' strategy was supported. In contrast, when disturbance was high and resources abundant, then a 'ruderal' strategy was supported. Finally, when disturbance was low and resources abundant, then a 'competitive' strategy was supported (Begon et al. 1996). Tilman (1988) in his mechanism based resource-ratio hypothesis of succession looked more specifically at the relationship between resource availability, of limiting soil nutrients and sunlight, and a plant specie's relative competitiveness (Begon et al. 1996). He proposed that soil nutrients would be low early in succession and, as time progressed, biomass would accumulate and decompose, both decreasing the available light and increasing the soil nutrient availability.

## GUILDS

To describe the structure and function of ecosystems, many researchers in recent years have emphasized functional classifications over traditional phylogenetic classifications (Gitay & Noble 1997). The idea of functional classification was first introduced by Root (1967), who used the term "guild" to represent a group of species that similarly exploited the same environmental resources (Begon et al. 1996). Since Root's introduction of the guild concept, there have been many related terms and definitions or extensions of the concept introduced by different people (Gitay & Noble 1997). Some of these include: functional grouping (Cummins 1974), modules (Paine 1980), and CSR strategies (Grime et al. 1988). Extensions of Root's initial guild concept include, assemblage and community guilds (Jaksic 1981), management guilds (Verner 1984), and functional, structural, and response guilds (Szaro 1986). There have also been suggestions made for subdivision and amalgamation of the basic guild concepts, including terms such as clique and dominant clique (Yodzis 1982), ecological species and ecological sector (Bahr 1982), league (Faber 1991), and functional analogues (Barbault et al. 1991). Despite the many different terms and definitions, they all share commonalties, the main difference among these approaches being the distinction between resource use or perturbation response (Gitay & Noble 1997). There is a further distinction among these, as to whether the shared resources are used by the species in the same way or differently, and likewise if the species response to perturbation is by the same mechanism or different mechanisms.

Functional guilds can be identified through subjective, deductive, or data-defined approaches (Gitay & Noble 1997). The subjective approach is based on observations of an ecosystem where it is assumed that functional guilds exist, with these groups forming the major descriptors of the environment, such as forest or grassland. Important descriptors for functional guild classification include physiognomy and life span (i.e. life form, *sensu* Raunkiaer 1934), dispersal mechanism, and shade, fire, and nutrient tolerance (Smith et al. 1993). Species can also be grouped according to their adaptive response to ecosystems. These would include resource use, response to disturbance and environment, stress tolerance, reproductive strategy, and phenology (Hobbs 1992).

For describing the impacts of disturbance, the use of guilds may represent an intermediate solution between complete compositional assessment and coarse scale measures of diversity (Hobbs 1997). Change in the relative importance of functional guilds can be measured to indicate response to disturbance and can be useful to predict future impacts (Hobbs 1997). For example, bird habitat assemblages were significantly related to forest condition in a study of anthropogenic disturbance (Canterbury et al. 2000). Life form has been used to monitor forest disturbance (McIntyre et al. 1995) whereas origin and habitat preference were related to species loss and compositional change associated with urban land use (Drayton & Primack 1996). Finally, flowering phenology and seed dispersal guilds were significantly related to species decline associated with human use (McLachlan & Bazely 2001).

## RIPARIAN FORESTS

The riparian landscape is a unique environment where the terrestrial habitat is strongly affected by, and in turn, affects the aquatic environment. This interaction is the most significant aspect defining riparian zones (Malanson 1993). The term 'riparian' in the traditional ecological concept implied 'affected by the river' (Malanson 1993); thus, the definition of riparian zones by Brown et al. (1979) was, 'an ecotone between aquatic and upland ecosystems' that is exposed to lateral water flow. Similarly the definition of riparian by Graf (1985) was simply 'in and near river channels and directly influenced by river-related processes'.

It has been recognized that riparian ecotones at a closer scale consist of both upland and aquatic ecotones, although most research has focused on the terrestrial – aquatic ecotone, and examined changes along this gradient (Malanson 1993). The riparian ecotone is variable, such that the terrestrial – aquatic gradient may be very short with a distinct separation of the two, or it may be spread over relatively greater distances. In areas where the two zones are not distinct, the change is usually characterized by a relation between topography and hydrological regime (Malanson 1993). For the purpose of this study, in examining the impacts of land use, I will focus more on the upland ecotone portion of the terrestrial-aquatic ecotone gradient.

Forests in these riparian zones represent an interface between soil, water, and vegetated systems, and play an important role in the river ecosystem structure and function (Gregory et al. 1991; Tabacchi et al. 1998; Brinson & Ver Hoeven 1999). Riparian forests stabilize riverbanks (Malanson 1993; Cordes et al. 1997), thus reducing sedimentation and protecting both water quality and aquatic habitat (Malanson 1993; Delong & Brusven 1998). Their frequent flooding leads to a species-rich ecosystem (Decamps & Tabacchi 1994), but these disturbances and their serpentine structure makes them highly susceptible to invasion by exotics (Planty-Tabacchi et al. 1996). In prairie landscapes, riparian forests are especially important features as they provide necessary habitat and cover for wildlife and act as corridors for dispersal (Cordes et al. 1997). They also significantly reduce sediment, nutrient and pesticide runoff, thus providing good quality water for watersheds in rural landscapes (Karr & Schlosser 1978; Lowrance et al. 1984; Malanson 1993). In urban environments, not only are they important for riverbank stabilization, but they provide many other primary and secondary benefits, often representing the only natural green-space for human health and enjoyment (Airola & Buchholz 1984). Riparian forests are recognized, however, as being threatened across North America (Knutson &Klaas 1998; Wissmar & Beschta 1998). If anthropogenic disturbance continues, their condition will likely further deteriorate, and their ecological recovery is unlikely without restoration attempts (Wissmar & Beschta 1998).

## STUDY AREA

This study was conducted on 25 fragmented riparian forest patches along the Assiniboine River in southern Manitoba (Fig 2.1, Appendix 1). The eastern most site (UTM Zone 14 634300E 5527500N) was located at the junction of the Assiniboine River with the Red River in downtown Winnipeg, whereas the western most site (UTM Zone14 583600E 5543800N) was located approximately 50 km west, just north of St. Eustache (Natural Resources Canada 1998). The study area is located at the southeast corner of the 520 000 square kilometer prairie ecozone, where agriculture currently represents 94 % of the land base (Wiken 1996). The landscape mosaic of grassland, aspen parkland and riparian forest was initially created after the recession of glacial Lake Agassiz approximately 9000 years ago (Shay 1984). Currently, remnant natural vegetation consists of greatly reduced patches of mixed and tall grass prairie, aspen parkland, and strips of riparian forest.

Riparian forest along the Assiniboine River was relatively unaltered during the early settlement of Winnipeg according to written descriptions, although little quantitative history exists (Warkentin 1964). A map of the Red River settlement (Fig. 2.2) shows that most of the early development occurred along the Red River, leaving extensive riparian forest along the Assiniboine River in present day Winnipeg (Arrowsmith 1819). Although there was extensive forest clearing around the "forks", for steamship fuelwood, continuous forest was shown to still exist west of Sturgeon creek, which became more dense west of Beaudry Provincial Park (Office of the Surveyor General 1921). Assessing change in riparian forest cover was easier after the 1940s when the federal government

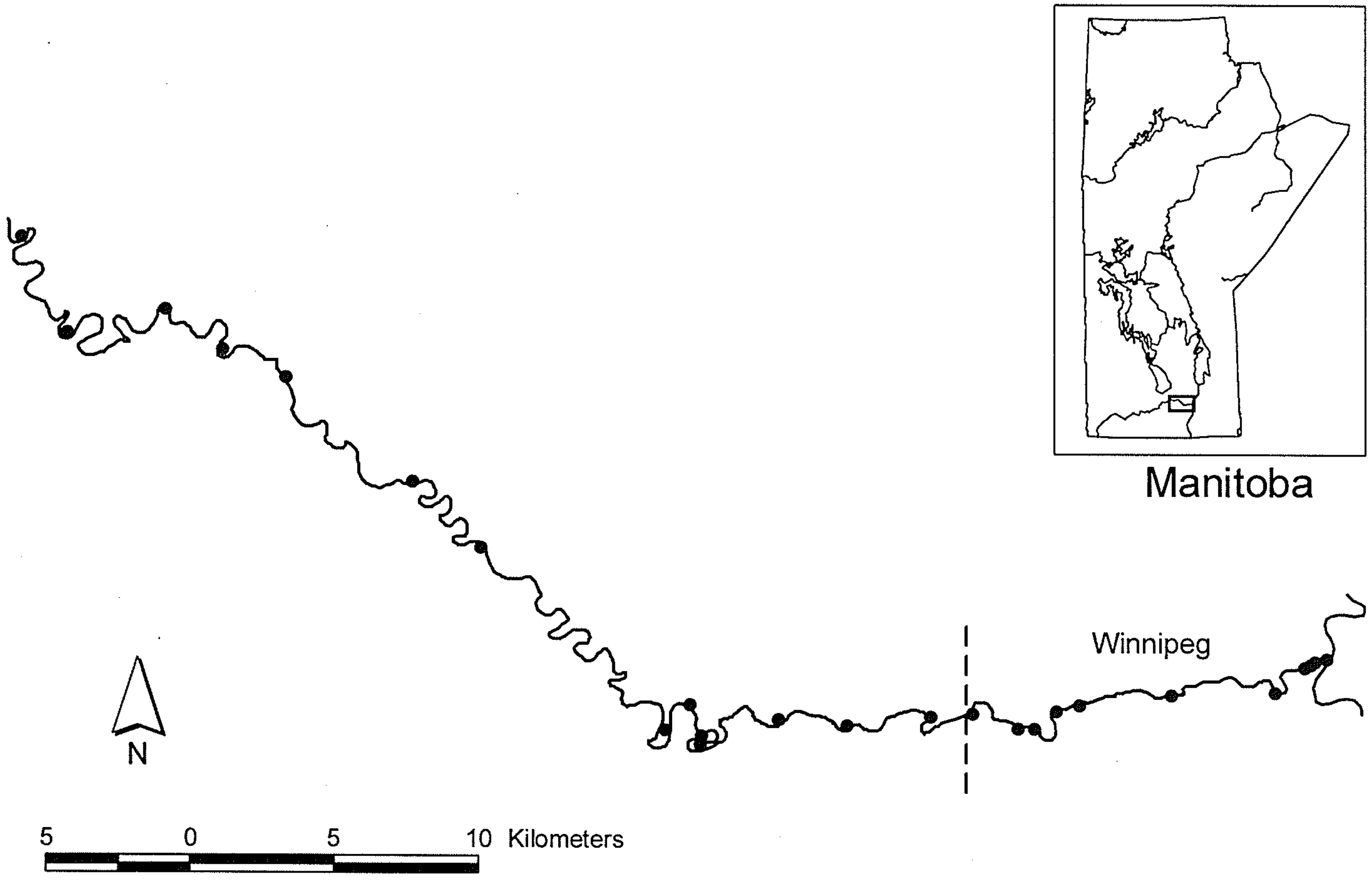


**Fig. 2.1**. Location of the 25 study sites along the Assiniboine River in Southern Manitoba (inset).

**Fig. 2.2**. Development of the Red River Settlement along the Red and Assiniboine Rivers in the early 1800s (Arrowsmith 1819).

began flying aerial photos of the area. In the 1948 photos, a continuous, albeit thin, strip of riparian forest remained in the downtown area, whereas in the suburban area beyond Munson Park, the forest cover was greater although not continuous (Government of Canada 1948). By 1959, with increased urban development of new buildings, roads, and bridges, there was a decline in the forest cover in the downtown area (Government of Canada 1959). By 1972, a large amount of the remnant forest west of Assiniboine Park had been cleared as Winnipeg expanded, with many new suburban subdivisions being built (Government of Canada 1972). The progressive fragmentation of, and decline in, riparian forest cover continued to present day. Currently, very little riparian forest remains within the city and that which does is very small and isolated.

Soil in the area is from the Red River Association of the Blackearth soil zone characterized as well to poorly drained. It overlies lacustrine clay and alluvial deposits that make up the Red River Plain of the Lake Agassiz Basin which, in turn, overlies Jurassic period sedimentary layers of shale (Ehrlich et al. 1953). The topography in the area is relatively flat, such that the Assiniboine River meanders across the landscape.

The climate is continental with an annual mean of 2.4 °C having a mean maximum of 26.1 °C in July and mean minimum of –23.6 °C in January (Environment Canada 1998). The mean annual precipitation is 504.4 mm; 404.4 mm falls as rain with the peak in June, while 100 mm water equivalent of snow falls annually with the peak in January.

# CHAPTER 3: Impacts of land use on riparian forest along an urban - rural gradient in southern Manitoba, Canada.

## 3.1 Introduction

The role of disturbance in determining plant community structure and function is now recognized as fundamental by plant ecologists. The effects of disturbance are difficult to understand because disturbance variables are often confounded with background environmental variables, background environmental variables are often correlated, and there is generally a lack of detail on prior disturbance (Motzkin et al. 1999). Disturbance can be defined as any event that alters the composition and structure of ecosystems, communities, or populations as a result of changes to the homeostatic range in resource availability and/or the physical environment (Godron & Formann 1983). Endogenous disturbance includes events such as natural flooding or wildfires, which plant communities have adapted to through repeated exposure, whereas exogenous disturbance often reflects more recent human modification to which communities largely are unadapted (Fox & Fox 1986). Although most ecological research has focused on endogenous disturbance, in light of extensive human-mediated changes in land use, exogenous disturbance is receiving increasing attention. Of the latter, fragmentation has been described as the greatest threat to, and cause of species extinction (Wilcox & Murphy 1985).

Fragmentation is described as the division of contiguous areas of native vegetation into smaller remnants or habitat islands separated by a matrix of different human land use (Saunders et al. 1991). Although research on forest fragmentation was initially influenced by the equilibrium theory of island biogeography (MacArthur & Wilson 1967) more emphasis is now placed on metapopulation theory (Levins 1970). The persistence of metapopulations are affected both by extinction of occupied patches and recolonization of unoccupied patches (Sih et al. 2000). Fragmentation affects patch size, shape, and connectivity and is characterized by habitat loss and the increased isolation of remnant habitat (Godron & Formann 1983).

Habitat loss leads to progressively smaller remnant natural patches and is associated with reductions in plant diversity (Airola & Buchholz 1984; Vogelmann 1995) and changes to plant population demographics including recruitment rates and size (Jules 1998). Fragmentation also is associated with a proportional increase of edge habitat (Vogelmann 1995). Forest edges tend to exhibit greater radiation, temperature, and water fluxes, as well as higher wind velocity. These effects are greatest on south or west facing edges (Saunders et al. 1991). Relative to forest interiors, these changes in microenvironment makes edges more susceptible to establishment by xeric and shade intolerant species as well as invasion by exotic species (Brothers & Spingarn 1992). Few studies, however, show changes in native species composition and interior conditions extending 20m beyond the forest edge (Murcia 1995).

As landscapes become fragmented, distances generally increase between remnant patches while any connecting corridors tend to be eroded (Brothers & Spingarn 1992). The degree of separation and connectivity has important implications for colonization and plant distributions in relation to seed dispersal (Primack & Miao 1992). As isolation increases, dispersal-restricted species such as ant, gravity, explosive, and wind dispersed species with heavy seeds, may become extirpated (Dzwonko & Loster 1992). This may also happen when the disperser is excluded from the matrix (Grashof-Bokdam 1997).

Many early successional, and exotic, plant species are effective dispersers under these fragmented conditions (Stylinski & Allen 1999).

Over the last three hundred years, landscapes across North America have become fragmented by agricultural use. There has been a consequent shift in land use from prairies and late-successional forests dominated by perennial species to relatively homogenous landscapes that are dominated by annual crop and weed species (Delong & Brusven 1998). These agricultural systems are generally intensively managed and require substantial nutrient and pesticide inputs (Lowrance et al. 1984). More recently, a shift in the economic base from one dependent on agriculture to one that includes industry and service (Dickinson 1966), has led to urban expansion and an associated conversion of cropland and natural habitat into urban land use (McDonnell & Pickett 1990). This expansion results in decreased patch size within cities and an increased isolation from other urban and rural remnant patches (Davis & Glick 1978). At a landscape scale, the degree of forest fragmentation can be predicted by human population density (Vogelmann 1995). Typically, extant urban forest is severely disturbed, especially by human trampling (Rudnicky & McDonnell 1989; Matlack 1997a). This disturbance is associated with removal of leaf litter, soil compaction, and a concomitant decline in native understorey species (Cole & Marion 1988; Kuss & Hall 1991) and increase in exotic and ruderal species diversity (Rudnicky & McDonnell 1989).

Extensive landscape modification has lead to a complex urban-rural gradient. This gradient, as an extension of Robert Whittaker's (1967) gradient paradigm, represents an important tool that can be used to address ecological questions at the landscape level of organization (Matson 1990; McDonnell et al. 1993). In particular, how patch size, shape, and isolation affect species composition and processes including seed dispersal (McDonnell & Pickett 1990). Urban-rural gradient studies show that urban land use is associated with a decline in forest species diversity, basal area, and canopy cover (Airola & Buchholz 1984), and an increase in exotic species diversity (Freedman et al. 1996). While the urban-rural gradient has also been used in studies of tree ring chemistry changes (Watmough et al. 1998), wildlife (Limburg & Schmidt 1990; Bowers & Breland 1996; Clergeau et al. 1998), water quality (Wear et al. 1998), and heavy metal accumulation in soils (Pouyat & McDonnell 1991), it has not, to my knowledge, been used to examine the impacts of land use on riparian forests.

Riparian forests represent an interface between soil, water, and vegetated systems, and play an important role in river ecosystem structure and function (Gregory et al. 1991; Tabacchi et al. 1998; Brinson & Ver Hoeven 1999). They stabilize riverbanks (Cordes et al. 1997), thus reducing sedimentation and protecting both water quality and aquatic habitat (Delong & Brusven 1998). Their frequent flooding leads to a species-rich ecosystem (Decamps & Tabacchi 1994), but also makes them highly susceptible to invasion by exotics (Planty-Tabacchi et al. 1996). In prairie landscapes, riparian forests provide important habitat and cover for wildlife and act as corridors for dispersal (Cordes et al. 1997). In urban environments, they often represent the only natural green-space for human health and enjoyment (Airola & Buchholz 1984) and reduce air pollution (Freedman et al. 1996). In rural landscapes, they significantly reduce nutrient and pesticide runoff (Lowrance et al.1984). Despite their importance, riparian forests are threatened across North America (Knutson & Klaas 1998). If this anthropogenic disturbance continues, these forests will further decline until their recovery is unlikely without active restoration (Wissmar & Beschta 1998).

The overall objective of this study was to assess the impact of surrounding land use on the fragmented riparian forests along the Assiniboine River using an urban-rural disturbance gradient. Specific questions I addressed were: 1) What changes in plant community species composition and diversity occur in response to the different land use? 2) What is the relative importance of the disturbance and environment variables in determining plant community species composition? 3) Does the land use gradient interact with the edge to interior gradient of the extant forest? I predict that the adverse effect of land use on riparian community composition and species richness will increase from rural to suburban use, and will be greatest in urban use. The effect of high intensity rural land use will be greater than that of low intensity rural land use. Finally, impacts of land use will be greatest at the terrestrial edge of the forest patches.

## 3.2 Methods

### SITE DESCRIPTION

This study was conducted on 25 fragments of riparian forest along the Assiniboine River in southern Manitoba (Fig 2.1, Appendix 1). The eastern-most forest patch (49°53'N, 97°08'W) was located at the junction of the Assiniboine River with the Red River in downtown Winnipeg, whereas the western-most (50°02'N, 97°50'W) was approximately 50 km west, located north of the town of St. Eustache. The study area is located at the southeast corner of the prairie ecozone, where agriculture currently represents 94 % of the land base (Wiken 1996). Remnant natural habitat is dominated by tall grass prairie characterized by *Andropogon gerardii*, *Sporobolus heterolepis*, and *Sorghastrum nutans* along with extant riparian forest. In the riparian forest important tree species include *Fraxinus pennsylvanica*, *Acer negundo*, *Tilia americana*, and *Ulmus americana*; important shrub species include *Rhus radicans*, *Symphoricarpos occidentalis*, *Parthenocissus quinquefolia*, and *Cornus stolonifera*; and important herbaceous species include *Taraxicum officinale*, *Smilacina stellata*, *Poa pratense*, *Smilax herbacea*, *Maianthemum canadense*, and *Bromus inermis* (Appendix 2).

Soil in the area is from the Red River Association of the Blackearth soil zone and is well to poorly drained. These soils overlie lacustrine clay and alluvial deposits that make up the Red River Plain of the Lake Agassiz Basin, which in turn overlies Jurassic period sedimentary layers of shale (Ehrlich et al. 1953). The climate of this region is continental with an annual mean temperature of 2.4°C, and ranges from a mean maximum of 26.1°C in July to a mean minimum of –23.6°C in January (Environment Canada 1998). The mean annual precipitation is 504.4 mm; 404.4 mm falls as rain which peaks in June, while 100 mm water equivalent of snow falls annually which peaks in January.

## SAMPLING DESIGN

### Site Level

Potential forest sites were identified along an urban-rural land use gradient using aerial photos from 1991 and 1994 (Linnet Geomatics International Inc. 1998). Sites were initially classified according to surrounding land use and include: i) urban sites (U) in the downtown core characterized by high rise office and apartment buildings (Fig. 3.1a); ii) suburban sites (S) located outside the downtown core, but within the city perimeter, and characterized by single family dwellings (Fig 3.1b); iii) high intensity rural sites (H) surrounded by cash crops subject to regular pesticide and fertilizer use (Fig. 3.1c); iv) low intensity rural sites (L) surrounded by forage crops not subject to pesticide and fertilizer use (Fig 3.1d); and v) reference sites (R) that are relatively large and generally perceived as high in quality – that is relatively intact. Once selected, each site was ground truthed to ensure the remnant patch still existed as depicted in the aerial photos and to confirm classification.

At each site, three line transects were randomly located perpendicular to the river, and at least 20 m apart and 50 m distance from any parallel forest edge. If the forest patch was wider than 250 m, then one transect was randomly located in each of three evenly divided sections. Along each transect, forest gradient strata were permanently marked at 0, 15, and 50 m from both the land and river edges of the forest patch, thus separating the forest into margin, edge and interior habitats, respectively. The 0 m mark for the land

**Fig 3.1**. Photographs of the interface between riparian forest patches and the surrounding land use; a) urban, b) suburban, c) High-intensity Rural, and d) Low-intensity Rural.

margin in each site was located at the point of edge maintenance, or treated as a canopy drip line edge (Ranney et. al 1981). To eliminate the confounding effects of annual flooding, the 0 m mark on the river margin was located at the high-water line. A seventh stratum was situated 5 m from the margin into the adjacent land use matrix.

At each forest gradient stratum, the species composition of herbs, defined as all herbaceous species and any woody plants shorter than 0.5 m in height, was recorded as percent cover from July 1 – August 31, 1999. Early flowering species were later identified from May 15 – July 15, 2000. Species were identified and categorized as native or exotic according to Budd's Flora of the Canadian Prairie Provinces (Looman & Best 1987). Two 2 x 1 m quadrats per stratum were situated along each transect whereas one of the three transects was randomly selected for an additional third quadrat, resulting in seven quadrats per stratum.

Woody species taller than 0.5 m and with a diameter at breast height (DBH) < 9 cm were defined as shrubs, while woody species taller than 0.5 m and with a DBH > 9 cm were defined as trees. Shrubs and trees were sampled from July 15 – August 31, 2000 along the three transects using a modified point-quarter method at each stratum. For each quarter at each stratum, species identity, DBH, and distance from the transect to the nearest shrub or tree were recorded. In addition, the distance from that shrub or tree to the next nearest shrub or tree, species identity, and DBH were recorded.

At each strata, I measured forest canopy cover, calculated by averaging values visually assessed from the four corners of each 2 x 1 m quadrat, topography, classified on a scale that ranged from flat (1) to ridge and swale (4), and aspect. In addition, edaphic variables were measured at each strata along the two transects without the third quadrat.

Percent soil moisture was calculated using soil cores (4 x 20 cm) collected on September 2, 2000, after a week of consistent temperatures and no rain. Soil samples were immediately weighed for wet mass and later oven-dried at 50°C for 24 hours in order 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 composition 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 et al. 1995). Peripheral and central selection was used to retain the maximum original variation of the soils, while ensuring that each of the 25 sites was represented. Soil composition of the reference samples was measured using the Bouycous Hydrometer Method (Karla & Maynard 1991).

### Landscape Level

Using aerial photographs, land use was digitized around each site using vector themes in ArcView 3.2. Land use was classified as urban (U), suburban (S), high intensity rural (H), and low intensity rural (L) land use as defined above. In addition, healthy forest (HF), degraded forest (DF), and river were also classified. Healthy forest was defined as any portion of a patch having a minimum dimension greater than 30 m and without a manicured or mown understorey. Degraded forest was defined as any portion of a patch with a minimum dimension between 10 m and 30 m, without a manicured or mown understorey. Any forest patches with a manicured understorey were classified according to contiguous land use. My land use classification was cross-referenced against classified 30 x 30 m LANDSAT imagery obtained from the Prairie Farm Rehabilitation Association (Agriculture & Agrifood Canada 1994, unpubl.). Any discrepancies between the two data sets were resolved using site visits and records of land use obtained from local landowners.

Proportions of each land use surrounding forest sites were measured using concentric circles with 100 m, 500 m, and 1000 m radii. Data within the 500 and 100 m circles ultimately were not used as they were highly correlated with 1000 m data, and because principal component analysis (PCA) indicated that 1000 m circles best discriminated between the five land use classifications. A measure of connectivity (Conn), modified from a spatial competition model for plants (Kenkel 1990), was calculated ($\mathrm{Conn} = \Sigma\, A_i^2\, (P_i\, D_i^2)^{-1}$, where A = patch area, P = perimeter, and D = center to center inter-patch distances) in order to assess the degree of isolation. Area:perimeter ratio (A/P) was calculated in order to assess shape in relation to fragmentation. Disturbance (Dstrb) was calculated for each site as a categorical variable, and ranged from no disturbance (1) to highly disturbed (10). Starting from 1 it was calculated using the 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 site (0 or 1) and the interior of the site (0 or 1).

## ANALYTICAL METHODS

Percent cover data of all individual herbaceous species, excluding the matrix stratum, were averaged for each of the 25 sites. Data were log transformed, in order to meet the assumptions of normality. Data were analyzed with correspondence analysis (CA), using

Canoco version 3.11 (Ter Braak 1990), in order to determine relationships between species composition and site land use classification along orthogonal axes of variation. Rare species were downweighted in importance during the analysis. Considering Oksanen and Minchin's (1997) discussion of stricter convergence criteria, which is missing in Canoco version 3.11, results from the CA ordination were confirmed using results generated by Podani's Syntax 5.0 (Podani 1994), which uses a more stable algorithm and is not susceptible to changes from data input order.

Urban (U), suburban (S), high intensity rural (H), low intensity rural (L), and reference (R) land uses were classified as categorical variables and used to constrain the species CA in a canonical correspondence analysis (CCA) (Ter Braak 1990). CCA visually shows the relationship among individual sites, species, and variables in a direct gradient analysis. For trees and shrubs, the relationship between sites, land use classification and species composition were also analyzed using CCA. The average DBH (cm) of each shrub and tree species was calculated for each of the 25 sites using point quarter data. These data were log transformed to meet assumptions of normality (Zar 1996), and rare species were down weighted.

Hill's (1973) diversity measures were used to examine the relationship between land use and species diversity. These include $N_0$, which examines the total number of species but is sensitive to rare species, and $N_2$, which is the reciprocal of Simpson's index and emphasizes dominance. Exotic, native and overall diversity of herbs and overall diversity of shrubs and trees were calculated for each of the 25 sites. Effects of land use on these diversity measures were analyzed using one-way analysis of variance (ANOVA) (SAS

Institute 1988). Post-hoc Tukey's tests (□ = 0.05) were used to separate means when overall treatment effects had been found significant.

Disturbance variables were averaged for each site and include connectivity, area:perimeter, patch size, site disturbance, canopy cover (Appendix 3), and the proportion of degraded forest, high rural, low rural, suburban, and urban land use within the 1000 m circle (Appendix 1). Effects of land use on disturbance variables were analyzed using ANOVA (SAS Institute 1988) and Tukey's test. Proportion of healthy forest and area were eliminated from further analysis because of their high correlation with connectivity and area: perimeter, respectively ($r > 0.90$). Aspect was also eliminated from this analysis as all sites exhibited similar overall aspect, and when averaged at the site level it has little ecological meaning.

To eliminate any confounding background natural variation associated with the underlying east to west distance gradient reflected in my study, environmental variables (Appendix 4) including pH, electrical conductivity, topography, percent sand, percent clay, and percent soil moisture, were regressed against distance from the junction of the Assiniboine and Red Rivers. As percent silt was highly correlated with percent sand and clay it was eliminated from regression analysis. Spearman rank correlations were calculated in order to describe the relationship between the disturbance and environmental variables, and their correspondence to land use classes.

Effects of land use on edge to interior pattern were investigated using CCA of herbaceous species composition constrained by the environmental variables. For each forest gradient stratum in each of the five land use categories, data were averaged, log transformed, and rare species down weighted. Although percent silt was highly correlated with percent sand and clay it was used at the strata level of organization, as it is meaningful when explaining differences between land and river margins. The only disturbance variable that was collected at the stratum level of organization, and thus used in the analysis, was canopy cover.

## 3.3 Results

### HERBACEOUS SPECIES

Land use was strongly related to herbaceous species composition. The 25 sites were tightly grouped around their respective centroids when constrained by the land use classification (Fig. 3.2a, b). CA axes 1-3 accounted for 16.3, 7.9, and 4.6 % of the variation, respectively, and, in total, accounted for 28.8 % of the variation within species data. When constrained, the species-environment correlations were 0.964, 0.854, and 0.944 for axis 1, 2, and 3, respectively. These correlations are meaningful, as the redundancy value (i.e., the proportion of the total variance from the CA explained when constrained by the environment variables) is high at 30.7 % (Økland 1999). All subsequent CCA exhibited similarly high redundancy values.

The five urban sites were grouped around their land use centroid (U) and were clearly separated from the remaining 20 sites along the first axis (Fig. 3.2a, b). Urban land use was characterized by five unique exotic and five unique native species. Of the former, *Solanum dulcamara* and *Hesperis matronalis* were very abundant whereas the remaining eight species were rarely encountered (Fig. 3.3). Urban sites were dominated by relatively few species, including *Parthenocissus quinquefolia* and *Arctium minus*. Although occurring in all the land use types, they were most prevalent in urban sites.

Similarly, the five suburban sites were grouped around their land use centroid (S) and were separated from the other sites along the second axis (Fig. 3.2a). Suburban land use was characterized by three unique exotic and nine unique native species (Fig. 3.3). Of the former, *Caragana arborescens* was frequently encountered, whereas the remaining eleven species were rare. Additionally, the exotic *Campanula rapunculoides* was strongly

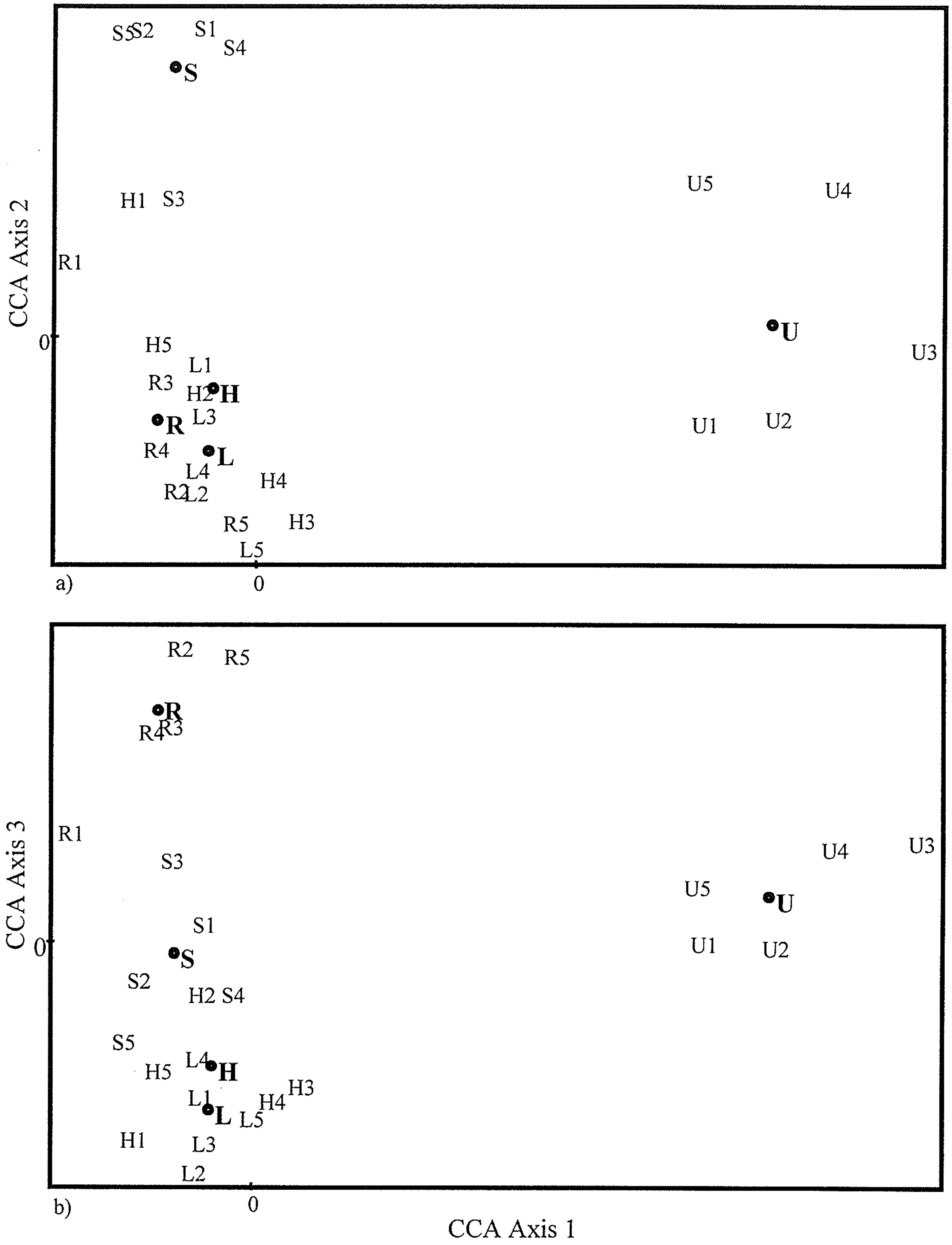


**Fig. 3.2**. Results of Canonical Correspondence Analysis (CCA) of N=25 sites, constrained by each land use class, showing the centroid (open circle) for (a) Axes 1 and 2, and (b) Axes 1 and 3. Land use classes are urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R).

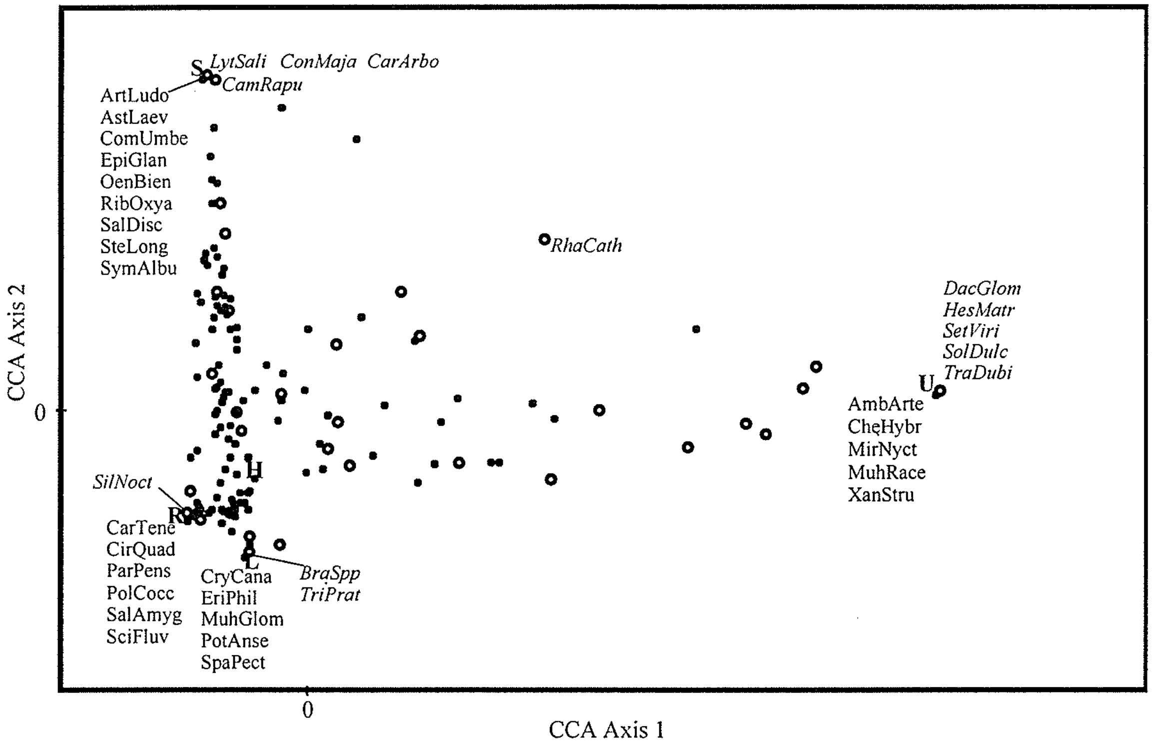


**Fig. 3.3.** Results of Canonical Correspondence Analysis (CCA) of N=179 herbaceous species, constrained by land use classification: urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R). Selected exotic (open circle, italicized) and native (closed box) herbaceous species are depicted, full names in Appendix 2.

associated with suburban land use, whereas the exotic *Rhamnus cathartica* was most prevalent in suburban and urban sites and rarely found elsewhere. One suburban site (S3) was distinct from the others, in large part responding to the presence of *Menispermum canadense* and *Matteuccia struthiopteris*, which were otherwise associated with rural land use.

The five reference sites separated from rural land use on axis three (Fig. 3.2b). Reference land use was characterized by one unique exotic and six unique native species (Fig. 3.3), although only *Scirpus fluviatilis* and *Polygonum coccineum* were frequently encountered. All these species, with the exception of the one exotic *Silene noctiflora* and *Parietaria pensylvanica*, were associated with wet site conditions. Additional hydrophilic species associated with reference sites included *Carex aquatilis* and the most dominant species in these sites, *Phalaris arundinacea*.

High and low intensity rural sites did not separate from each other and were generally found near the zero region of the ordinations (Fig. 3.2a, b). Although both land uses had unique species, they were encountered infrequently (Fig. 3.3). The dominant plant species in rural sites was the exotic *Bromus inermis*, although it was also very dominant in all other land uses except for suburban sites. In addition, rural land use was frequently associated with *Melilotus alba* and *Phryma leptostachya*.

Land use also strongly affected herbaceous species diversity (Table 3.1). Urban sites had < 50 % of the overall total species richness and the number of dominants compared to other land uses. Although differences were less significant among the other four land use types, reference sites had a higher overall species richness, and low rural sites had a

**Table 3.1**. Mean Hill diversities; species richness ($N_0$) and dominant species ($N_2$) of all, exotic, and native herbaceous species, all shrub species, and all tree species for each land use category (N = 5). Means separated using Tukey's HSD, and with *P* values from one-way ANOVAs of land use.

| | | | Land use category | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Urban | Suburban | High rural | Low rural | Reference | *P* † |
| Herbaceous | Overall | $N_0$ | 33.2 b | 71.2 a | 67.0 a | 67.8 a | 72.6 a | < 0.0001 |
| | | $N_2$ | 4.8 b | 11.9 ab | 9.0 ab | 14.8 a | 11.6 ab | 0.0320 |
| | Exotic | $N_0$ | 13.0 | 13.2 | 10.4 | 12.8 | 7.6 | NS |
| | | $N_2$ | 3.0 | 3.4 | 2.5 | 2.3 | 2.9 | NS |
| | Native | $N_0$ | 20.2 b | 58.0 a | 56.6 a | 55.0 a | 65.0 a | < 0.0001 |
| | | $N_2$ | 3.4 b | 9.5 ab | 9.4 ab | 13.7 a | 11.3 ab | 0.0125 |
| Shrub | Overall | $N_0$ | 8.4 b | 15.8 a | 15.4 a | 12.8 ab | 14.8 a | 0.0012 |
| | | $N_2$ | 3.3 b | 6.7 a | 5.9 ab | 4.9 ab | 6.0 ab | 0.0261 |
| Tree | Overall | $N_0$ | 5.0 | 6.6 | 7.2 | 7.0 | 7.0 | NS |
| | | $N_2$ | 2.9 | 2.8 | 4.3 | 3.8 | 3.6 | NS |

† NS, not significant ($P > 0.05$).

higher number of dominant species. Urban and suburban sites had the highest exotic species richness and suburban sites had the largest number of dominant exotics. Urban sites also had less than 30 % of the native species richness and number of dominant natives compared to reference sites, whereas suburban sites exhibited little difference. In contrast, reference sites had the lowest exotic and the highest native species richness, and low rural sites had the fewest exotic and the most native dominant species.

## SHRUB AND TREE SPECIES

Land use was related to shrub species composition, although less strongly than to herbaceous species (Fig. 3.4a). The first two CA axes accounted for 19.5 % and 10.2 % of the variation, respectively, for a cumulative 29.7% of the variation within species data. When constrained, the species-environment correlations for axes 1 and 2 are 0.932 and 0.839, respectively.

The five urban sites separated from the other sites along the first axis, although they were weakly grouped along the second axis (Fig. 3.4a). These sites were characterized by a unique and frequently occurring exotic species, *S. dulcamara*, and a third exotic species, *R. cathartica*, which is also strongly associated with suburban use. The most dominant species in urban sites was the native *Acer negundo*, which also was found in all other land uses, though at a relatively lower abundance and dominance.

The five suburban sites separated from the other sites along the second axis, but again they were weakly grouped (Fig. 3.4a). The abundant exotic *C. arborescens* was unique to suburban land use. The two most dominant species in suburban sites, *Amelanchier alnifolia* and *Prunus virginiana*, favoured suburban sites, while the exotic

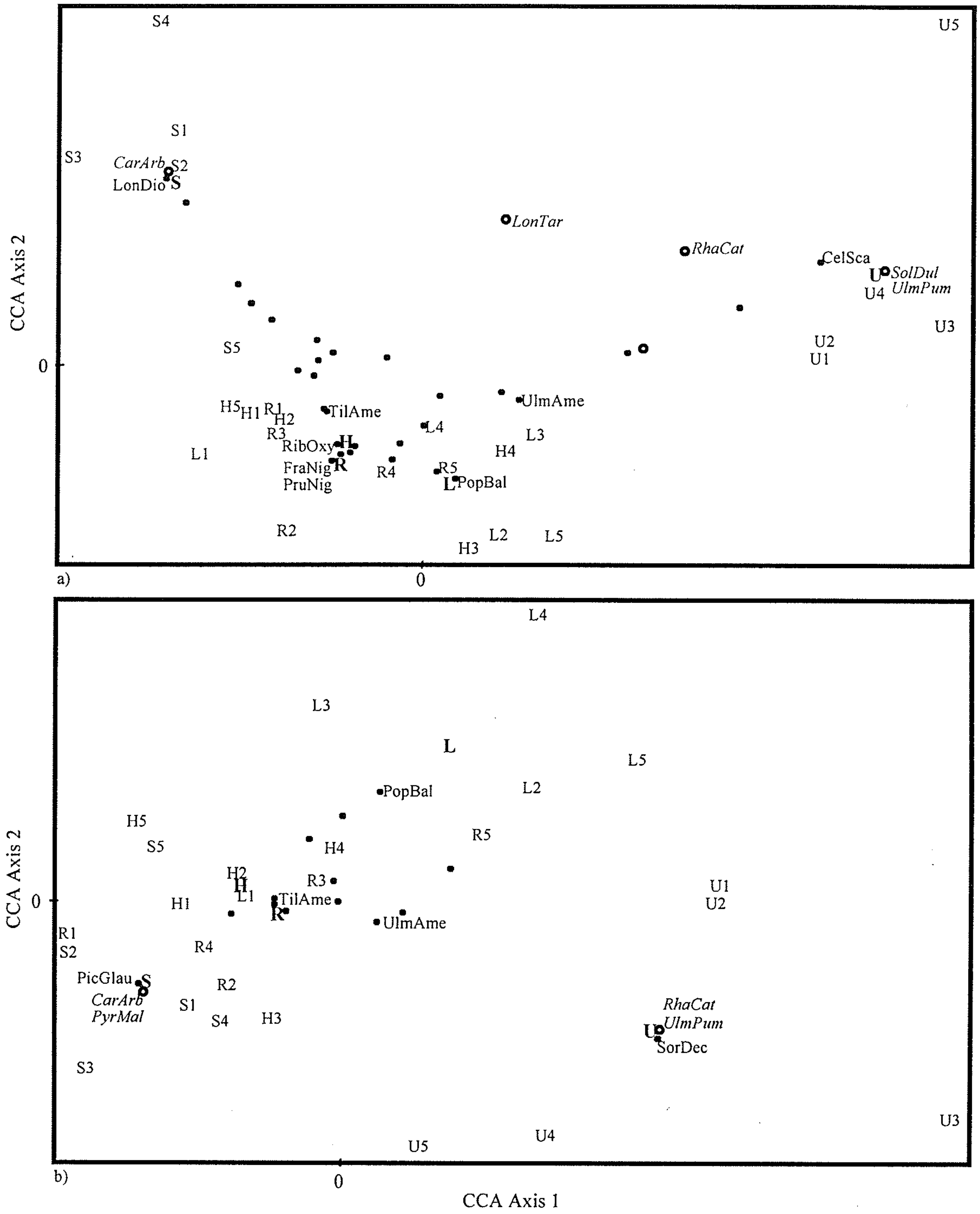


**Fig. 3.4**. Results of Canonical Correspondence Analysis (CCA) of N=25 sites, constrained by land use classification. Land use classes are urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R). Selected exotic (open circle, italicized) and native (closed box) species are depicted for (a) N=36 shrubs and (b) N= 18 trees, full names are listed in Appendix 2.

*Lonicera tartarica* occurred equally abundantly in urban and suburban sites and was absent from all other land uses. The suburban site S5 was more closely grouped to the rural sites, in part responding to the absence of *L. tartarica*, in addition to having higher abundance of *Fraxinus pennsylvanica*, relative to other suburban sites.

High rural, low rural, and reference sites did not separate from each other and were loosely grouped around their respective centroids (Fig. 3.4a). The native species *Ribes oxycanthoides*, *Populus balsamifera*, and *Fraxinus nigra* and *Prunus nigra* were unique, albeit infrequent, to high rural, low rural, and reference sites, respectively. All three land use types were dominated by *F. pennsylvanica* and the slightly less abundant *Ulmus americana*, *Tilia americana*, and *A. negundo*.

Land use was only weakly related to tree species composition, as the 25 sites were poorly separated when constrained by their respective land use classification (Fig. 3.4b). Whereas CA axis 1 accounted for 21.0 %, axis 2 only accounted for 6.4 % of the variation. When constrained, the species-environment correlations were relatively low at 0.810 and 0.764 for axes 1 and 2, respectively.

Only urban land use weakly separated from other land uses, in part because 6 of the 18 tree species occurred across all land uses (Fig. 3.4b). Two exotics and one native species were unique to urban sites, although only *Ulmus pumila* was found in any abundance. Urban sites were dominated by *A. negundo* and *U. americana* and characterized by the relative absence of *T. americana*.

There was little difference between the other four land use types responding to tree species composition (Fig. 3.4b). Although they differed in their relative ranking, *Quercus macrocarpa, F. pennsylvanica, Populus deltoides, T. americana*, and *A. negundo* were all the most abundant species found at each of these land uses. Three infrequent exotic species, *C. arborescens*, *Pyrus mallus*, and *Picea glauca*, were unique to suburban sites and the infrequent *F. nigra* was unique to reference sites.

Shrub and tree species diversity was also affected by land use (Table 3.1). Urban sites had a lower overall shrub species richness, nearly half that of the other land uses, except for low rural use. Urban sites also had significantly fewer dominant shrub species than the other land uses, again, except for low rural use. In contrast, tree species diversity showed a weaker response to land use, as only urban sites had lower species richness.

## LAND USE CHARACTERIZATION

Sites categorized as urban (U) were predictably associated with urban cover (80.1 %) ($P < 0.001$) (Table 3.2, Table 3.3). Urban riparian forests were highly fragmented, and due to their small size and low area:perimeter ratio ($P < 0.001$), they lacked interior habitat. These patches were also extremely isolated and the few forests surrounding them were degraded, thus they exhibited a low mean connectivity value ($P < 0.001$). In addition, these sites were severely disturbed relative to other land uses ($P < 0.001$).

Sites classified as suburban (S) predictably were characterized by suburban land use (74.3 %) ($P < 0.001$) (Table 3.2, Table 3.3). Although highly fragmented, they were larger than urban sites, had higher area:perimeter ratios and, thus, exhibited interior habitat. Although still surrounded by degraded forests, suburban sites were closer to rural land use ($P < 0.05$) and, thus, were more connected. Suburban sites were still severely disturbed, although less so than urban sites.

**Table 3.2**. Site characterization and measure of landscape and site level disturbance for each land use category (N=5). Means are separated using Tukey's HSD, and with *P* values from one-way ANOVAs of land use.

| | Land use category | | | | | |
|---|---|---|---|---|---|---|
| | Urban | Suburban | High rural | Low rural | Reference | *P* † |
| Percent urban land use | 80.1 | 0.0 | 0.0 | 0.0 | 0.0 | |
| Percent suburban land use | 6.2 | 74.3 | 4.4 | 0.9 | 15.7 | |
| Percent high intensity rural land use | 0.0 | 1.9 | 57.3 | 62.3 | 20.8 | |
| Percent low intensity rural land use | 0.0 | 5.7 | 11.3 | 12.6 | 19.5 | |
| Percent degraded forest | 3.1 | 3.4 | 2.5 | 1.8 | 1.3 | NS |
| Disturbance‡ | 9.2 a | 6.8 a | 3.4 b | 3.0 b | 4.0 b | < 0.0001 |
| Forest patch size (ha) | 0.5 b | 4.7 b | 14.9 b | 16.1 b | 47.1 a | < 0.0001 |
| Area:Perimeter | 13.4 c | 28.2 bc | 47.2 b | 43.7 b | 77.9 a | < 0.0001 |
| Connectivity§ | 1.9 b | 20.2 ab | 66.1 ab | 41.3 ab | 281.7 a | 0.0308 |
| Percent canopy cover | 75.3 | 69.9 | 69.6 | 70.2 | 65.2 | NS |

† NS, not significant ($P > 0.05$).

‡ Disturbance, measured from no disturbance (1) to severe disturbance (10) based on abundance of trails and garbage, and accesability

§ Connectivity is calculated based on the area and perimeter of and distance to surrounding remnant forest patches

**Table 3.3**. Correlations among the disturbance and environment variables: |r| > 0.42, > 0.53, and > 0.65 are significant at $P < 0.05$, < 0.01, and < 0.001 respectively. The bottom panel shows the correlation of these variables to the five land use categories.

| | Proportion of surrounding cover | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | U | S | DF | H | L | Dstrb | A/P | Conn | CanCov | %SM | pH | Ec | Topo | Sand | Clay |
| Urban | 1.00 | | | | | | | | | | | | | | |
| Suburban | 0.20 | 1.00 | | | | | | | | | | | | | |
| Degraded Forest | 0.26 | 0.63 ** | 1.00 | | | | | | | | | | | | |
| High rural | -0.53 ** | -0.76 *** | -0.47 * | 1.00 | | | | | | | | | | | |
| Low rural | -0.53 ** | -0.65 *** | -0.48 * | 0.60 ** | 1.00 | | | | | | | | | | |
| Disturbance† | 0.69 *** | 0.73 *** | 0.61 ** | -0.85 *** | -0.65 *** | 1.00 | | | | | | | | | |
| Area:Perimeter | -0.65 *** | -0.58 ** | -0.58 ** | 0.61 ** | 0.69 *** | -0.76 *** | 1.00 | | | | | | | | |
| Connectivity‡ | -0.69 *** | -0.51 * | -0.46 * | 0.42 * | 0.83 *** | -0.66 *** | 0.73 *** | 1.00 | | | | | | | |
| % Canopy Cover | 0.26 | 0.13 | 0.28 | -0.05 | -0.3 | 0.22 | -0.4 | -0.4 | 1.00 | | | | | | |
| % Soil Moisture | -0.65 *** | -0.16 | -0.10 | 0.36 | 0.23 | -0.40 | 0.47 * | 0.45 * | -0.29 | 1.00 | | | | | |
| pH | 0.61 ** | 0.03 | 0.05 | -0.27 | -0.6 ** | 0.24 | -0.5 * | -0.5 ** | 0.36 | -0.58 ** | 1.00 | | | | |

**Table 3.3**. Cont'd

| | Proportion of surrounding cover | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | U | S | DF | H | L | Dstrb | A/P | Conn | CanCov | %SM | pH | Ec | Topo | Sand | Clay |
| Ec | -0.04 | -0.34 | -0.17 | 0.22 | 0.24 | -0.07 | 0.16 | 0.23 | -0.09 | 0.40 | -0.40 | 1.00 | | | |
| Topography | 0.64 ** | 0.13 | 0.22 | -0.50 * | -0.6 ** | 0.46 * | -0.5 * | -0.5 * | 0.15 | -0.46 * | 0.74 *** | -0.13 | 1.00 | | |
| Percent Sand | -0.06 | 0.64 ** | 0.26 | -0.39 | -0.3 | 0.36 | -0.3 | -0.2 | -0.30 | 0.15 | -0.34 | -0.17 | -0.17 | 1.00 | |
| Percent Clay | 0.37 | -0.25 | 0.11 | -0.07 | 0.23 | 0.21 | -0.1 | 0.03 | 0.02 | -0.38 | 0.16 | 0.27 | 0.34 | -0.6 ** | 1.00 |
| Urban | 0.99 *** | 0.20 | 0.28 | -0.54 ** | -0.54 ** | 0.69 *** | -0.67 *** | -0.69 *** | 0.24 | -0.66 *** | 0.62 ** | -0.04 | 0.65 ** | -0.06 | 0.37 |
| Suburban | -0.25 | 0.69 *** | 0.30 | -0.46 * | -0.29 | 0.33 | -0.31 | -0.06 | 0.01 | 0.04 | -0.13 | -0.35 | -0.13 | 0.43 * | -0.19 |
| High rural | -0.25 | -0.27 | 0.01 | 0.43 * | 0.24 | -0.36 | 0.24 | 0.28 | -0.04 | 0.32 | -0.31 | 0.22 | -0.40 | 0.04 | -0.14 |
| Low rural | -0.25 | -0.42 * | -0.19 | 0.57 ** | 0.23 | -0.43 * | 0.17 | 0.06 | -0.01 | 0.16 | 0.07 | 0.10 | 0.01 | -0.42 * | 0.10 |
| Reference | -0.25 | -0.21 | -0.39 | -0.01 | 0.35 | -0.24 | 0.57 ** | 0.42 * | -0.19 | 0.15 | -0.26 | 0.07 | -0.13 | 0.01 | -0.14 |

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$: others not significant $P > 0.05$.

† Disturbance, measured from no disturbance (1) to severe disturbance (10) based on abundance of trails and garbage, and accesability

‡ Connectivity is calculated based on the area and perimeter of and distance to surrounding remnant forest patches

High rural (H), low rural (L), and reference (R) sites were all located in a rural land use matrix, and thus, characterized by similar proportions of surrounding land use (Table 3.2). Forests in these three land use categories were still fragmented, though much less than urban and suburban sites, and also exhibited less degraded forest. The area of reference sites was 100x, 10x, and 3x larger than urban, suburban, and rural sites respectively. Similarly, their area:perimeter ratio ($P < 0.01$) was substantially larger than the other land uses (Table 3.2, Table 3.3). Reference sites had the least degraded forest and were the most connected ($P < 0.05$), exhibiting 150x and 14x higher connectivity values than those of urban and suburban sites, respectively. Finally, high rural, low rural ($P < 0.05$), and reference sites all have lower disturbance values than urban and suburban land use.

The land use gradient also represents an underlying east to west distance gradient. Of the six tested variables only percent sand ($P = 0.0043$) and percent soil moisture ($P = 0.0279$) showed a significant relationship with distance from the river junction (Table 3.4). However, these variables also reflected a response to changes in land use. Percent sand was positively correlated with suburban land use ($P < 0.05$) and negatively correlated with low rural land use ($P < 0.05$), whereas percent soil moisture was negatively correlated with urban land use ($P < 0.001$) (Table 3.3). Topography and pH were both positively correlated with urban land use ($P < 0.01$).

## EDGE-INTERIOR RESPONSE

Impacts of land use on the species composition were contrasted for edge and interior portions of the forest patches. Herbaceous species composition exhibited a distinct land margin to river margin structure (Fig. 3.5). CA axes 1and 2 accounted for 13.5 % and

**Table 3.4**. Results for regression of environmental variables with distance gradient from city centre (0 km) to the western most site (~50 km).

| | Equation | $F_{1,23}$ | $r^2$ | *P* † |
|---|---|---|---|---|
| Electrical conductivity | y = 0x + 0.15 | 0.00 | 0.00 | NS |
| pH | y = -0.003x + 7.68 | 0.25 | 0.01 | NS |
| Percent Clay | y = -0.03x + 26.29 | 0.26 | 0.01 | NS |
| Percent Sand | y = -0.23x + 29.56 | 10.00 | 0.30 | 0.0043 |
| Percent Soil Moisture | y = 0.06x + 22.18 | 5.51 | 0.19 | 0.0279 |
| Topography | y = -0.008x + 2.29 | 3.23 | 0.12 | NS |

† NS, not significant ($P > 0.05$).

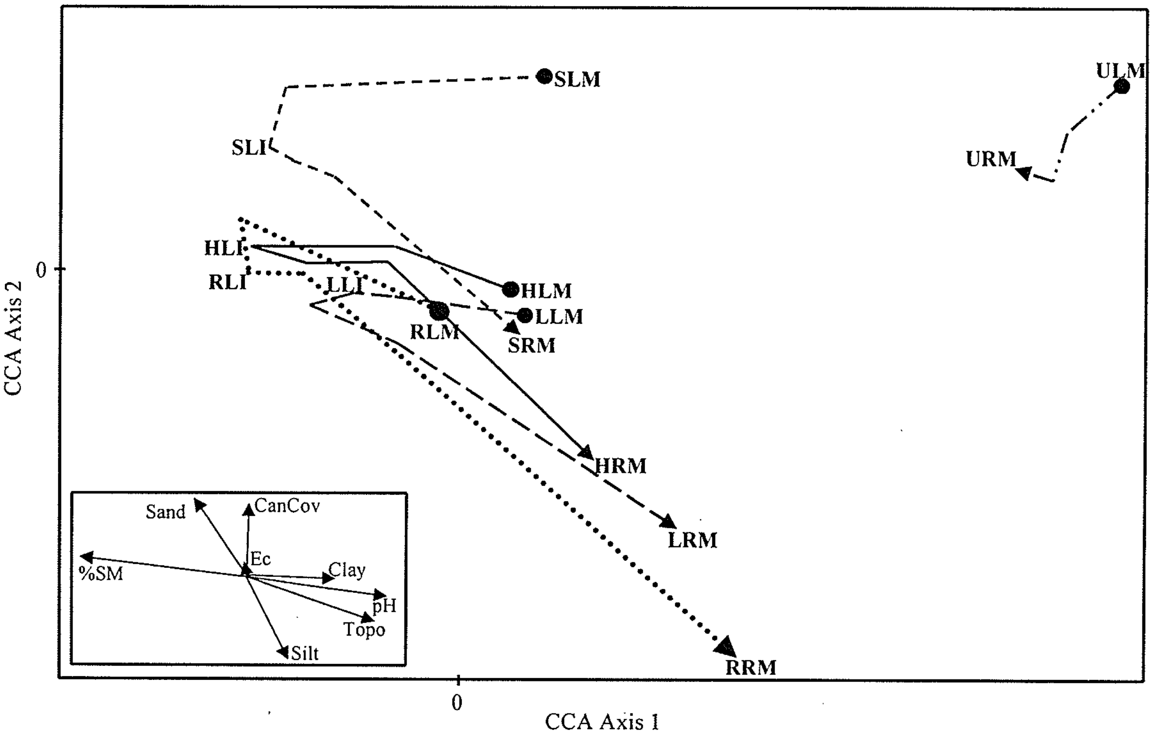


**Fig. 3.5**. Results of Canonical Correspondence Analysis (CCA) of N=28 land use forest gradient strata, constrained by environment variables (inset). Vectors show transition from land margin (LM) through the land interior (LI) to river margin (RM) for urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R) land use categories.

11.3 % of the variation, respectively, explaining a cumulative 24.8 % of the variation within species data (Fig. 3.5). When constrained, the species-environment correlations were 0.888 and 0.887 for axis 1 and 2, respectively.

The urban strata were clearly separated from the other land use strata along the first axis (Fig. 3.5). Urban land use lacked interior strata, and exhibited a different land margin (LM) to river margin (RM) pattern than the four other land use categories. As with the site-level analyses, the separation of urban land use along axis 1 was associated with such exotics as *Solanum dulcamara* and *Hesperis matronalis*. These urban strata were associated with relatively dry and alkaline soils and sloping topography (Fig. 3.5). Although the variation between strata within urban land use is small relative to the variation between urban and the other land uses, there was a slight gradient from land to river margin associated with a decrease in percent sand and canopy cover, and an increase in percent silt.

In contrast, all other land use strata had a distinct land margin to river margin pattern (Fig. 3.5). This general pattern represented a gradient from land margin to interior that was associated with an increase in soil moisture. Species associated with these interior strata included *Carex assinaboinensis*, *C. springelli*, and *C. pensylvanica*. The gradient towards river margin strata was associated with a more open canopy, increased ridge and swale topography, and soils with increased percent silt. Species associated with river margins were hydrophilic and included *C. aquatilis*, *Salix amygdaloides*, *S. interior*, and *Phalaris arundinacea*. Suburban strata separated from other land use types along axis 2 and exhibited higher canopy cover and sandier soils. Two exotic species, *Caragana*

## 3.4 Discussion

### LAND USE RESPONSE

My study showed that land use had a substantial impact on the riparian forests along the urban rural gradient. Urban land use had the greatest effect on species composition and diversity, whether herbs, shrubs or to a lesser extent trees, which reflects the findings of other studies (e.g., Hoehne 1981; Airola & Buchholz 1984; Freedman et al. 1996). Additionally, urban land use had the most adverse effect on the edge to interior pattern of the remnant patches. Although the effects of suburban land use were not as severe as urban, they did alter the species composition and diversity as well as edge to interior pattern.

Extant urban forest in Winnipeg consists of extremely small and isolated regenerating secondary-forest. Because of their small size, urban forest patches generally lack interior habitat. Core area declines sharply with decreasing fragment size and edge effects increase exponentially once a varying critical size is surpassed (Laurance & Yensen 1991). There is little agreement of the depth of edge effects in the literature (Murcia 1995), and the minimum critical patch size required to retain interior habitat ranges from 1ha (Fraver 1994) to 3.8 ha (Levenson 1981). Regardless, these estimates are substantially larger than the 0.5 ha mean size exhibited by urban forests in my study. In addition, urban riparian forests situated along the Assiniboine River are secondary, as they were largely cleared less than 100 years ago for construction and fuel wood (C. Hemming pers. comm.). Forests surrounding Philadelphia were similarly cleared as wood was rarely transported more than 40-50 km to an urban center during that time period

(Matlack 1997b). Although urban forests may regenerate, this leads to relatively large stands of secondary forest consisting of mostly edge habitat (Matlack 1997a).

As extant urban forest in my study consisted entirely of edge habitat, the species composition was very different from that of other land uses, and reflected a much higher percentage of exotic species. The species composition of the urban seed bank was also dominated by exotics (Chapter 4). Generally, the proportion of exotic species tends to increase in small and edge dominated stands (Burke & Nol 1998). Edge-to-interior studies also have shown that the number of ruderal and exotic species is higher at edges, and tends to decline toward the interior (Fraver 1994). The dominance of exotic species also helps explain why urban forests lacked any strong land to river margin pattern.

The poor quality of extant urban forest also was reflected by lower herb, shrub, and tree species diversity. Secondary forests are typically species impoverished, as restrictions in dispersal, characteristic of many understorey species, may prevent colonization of even slightly isolated patches (Dzwonko & Loster 1992). This lower diversity was not as evident for trees, in part because they have greater longevity, are less vulnerable to disturbance, and colonize disturbed areas more effectively than do herbaceous species (Matlack 1994b).

Compared to urban forest, extant suburban forest in my study area had interior habitat and historically were not entirely cleared (C. Heming, pers. comm.). Although these patches were still disturbed, the effects of suburban land use were less severe than that of urban land use. Suburban development results in the ongoing clearing of forest patches. Indeed over the last seven years, more than half of the remnant suburban patches had been extensively modified or removed (S. Moffatt pers. obs.). Suburban forest remnants are generally isolated, small and thin, and characterized by a high proportion of edge habitat (Vogelmann 1995). As with urban sites, these increases in edge habitat are responsible for the higher diversity of exotic herbs. However, the interior of these suburban sites was largely intact and had a native diversity similar to that of rural forests. The importance of this interior habitat was also reflected in the edge to interior pattern exhibited by suburban forests. Although this pattern resembled that of rural forests, suburban patches were characterized by a greater proportion of exotic species, and, in particular, escaped horticultural species.

I categorized forest sites as high and low intensity rural and reference land use, and it was anticipated that the large and highly connected reference sites would have the highest ecological integrity. Reference sites were associated with hydrophilic species, in part explaining their prominence in this human-dominated landscape. That these sites were likely too wet to be drained and effectively converted to agricultural use, might thus explain their continued presence and relatively large size. Otherwise, they generally showed a similar diversity, species composition, and edge to interior pattern to high and low intensity rural sites. The similarities in these three land use types, in part, reflect the similar surrounding rural matrix, although it is likely that they have all been reduced in size and degraded by this rural land use. I further anticipated that the species composition and diversity of high intensity rural forests would be distinct from those of low intensity forests. Although other studies have suggested that high intensity rural land use results in a decline in native species and an increased proportion of annual and biennials along the land edge (e.g., Boutin & Jobin 1998); there was little difference between these land use types in my study sites.

## IMPORTANCE OF DISTURBANCE AND ENVIRONMENTAL VARIABLES

The disturbance variables used to characterize land use and to interpret changes in species composition were effective, as many were significantly associated with at least one or more of the land use categories. Similar variables have been used in other studies that related land use to species diversity and composition (e.g., Miller et al. 1997), and reflected four of the six general measures of landscape pattern identified by Ritters et al. (1995). Both connectivity and area:perimeter measures used in my study were positively correlated with a change from urban to rural land use. Landscape indices incorporating changes in area and perimeter are the best predictors of seed dispersal success and affect species composition and diversity (Schumaker 1996). Other studies of urban/suburban environments also show that habitat size, isolation, and patch density, are related to plant species composition and richness (e.g., Bastin & Thomas 1999).

Environmental variables were not as effective at assessing impacts of land use, as few were significantly correlated with the land use categories. Percent soil moisture, topography, and pH were associated with urban land use. The higher pH of urban soils is likely a response to the higher carbonates in the soil from discarded building materials such as gypsum and concrete. Other studies have also found that soil of urban sites are drier than those surrounded by rural use (e.g., White & McDonnell 1988). The modified landscape of urban environments, comprising concrete surfaces along with a drainage infrastructure, quickly drains water after rain events. In addition, percolation is prevented as a result of the highly compacted urban soils, and compaction from trampling generally increases with human use (e.g., Cole & Marion 1988; Kuss & Hall 1991). Percent sand was associated with suburban land use, and may reflect the continuing building activity of suburban expansion. The higher percent sand of suburban soils may also be related to continental climate of my study area, where the large amounts of sand applied to city roads through the winter is blown into adjacent forest patches.

Although my study clearly represented an urban-rural gradient, it also reflected a potentially confounding east to west gradient. When tested, only percent soil moisture and percent sand showed any significant change along this directional gradient, and, as previously discussed, both of these are strongly related to land use disturbance.

The strong inter-correlation between disturbance and environmental variables, in large part, was due to their relationships with land use. For example, percent soil moisture, pH, and topography, were all strongly correlated with the urban land use category, and, in turn, were correlated with proportion of urban cover, area:perimeter, and connectivity. In contrast, Motzkin et al. (1999) were unable to separate the relative importance of environmental conditions and disturbance history for vegetation patterns in rural landscapes. Despite the relationship between disturbance and environmental variables, the strength and frequency of the relationships between disturbance variables and land use were greater than those for environmental variables. This suggests that landscape measures of disturbance may be confidently used to assess the impacts of land use in vegetation studies, especially along urban-rural gradients.

## CONCLUSION

This study represents a gradient of increasing disturbance from rural, to suburban, and, finally, urban land use. Disturbance contributes to the decline of the native understorey and promotes the establishment of invasive exotic species in riparian forest systems (Pyle 1995). The latter may, in turn, prevent the regeneration of native species

(Stylinski & Allen 1999). This is especially true of human-mediated disturbance, as many Eurasian exotics have evolved in response to human land use (Forcella & Harvey 1983). I have shown that urban land use has had the greatest adverse effects, and the introduction of exotics is associated with changes in native species composition and declines in diversity.

My study, like many that examine habitat fragmentation, may be limited by the number of replicates for each land use type. However, all the appropriate urban and suburban sites were sampled. Indeed, the limited number of sites was an indicator of land use disturbance. Another potential problem was the small size of urban sites that excluded interior habitat. Although the lack of interior may have been responsible for differences in species composition and diversity between urban and non-urban sites, this reflects the intensity of the surrounding land use. Moreover, when interior samples were removed from all sites and species composition was compared, the distinction between urban and non-urban sites remained, suggesting that the absence of interior habitat at urban sites was, in of itself, an inadequate explanation for differences exhibited by these land uses. Additional effects of downriver cumulative "disturbance loading", whether they be siltation, nutrient concentration, or pesticide concentration, warrant further investigation.

To my knowledge, no study has looked at the effects of land use along an urban-rural gradient on riparian forests and certainly none in prairie landscapes. This project represents an important first step for the management of riparian forests as it has generated much needed information regarding the severity of land use. My multi-scale study benefited from incorporating both landscape level and site-level variables when describing the impacts of this urban-rural gradient on vegetation. This methodology is likely applicable to remnant habitat in other human-dominated landscapes. However, the relationship between landscape level disturbance variables and land use was strong enough that the former might be used to develop management plans for fragmented riparian forests.

# CHAPTER 4: Seed bank of riparian forests in Southern Manitoba; effects of land use disturbance along an urban-rural gradient.

## 4.1 Introduction

The importance of seed banks for the maintenance and regeneration of plant communities is increasingly recognized. Their size and role in life history makes them more important than the bud and propagule reproductive banks for plant community studies (Simpson et al. 1989). Information on seed banks also 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 been on arable or post-arable land and few have examined the effects of surrounding 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, their seed bank composition changes from short to long-lived species, and seed bank species diversity and seed density both decrease (Roberts & Vankat 1991). Environmental factors can also affect forest seed banks. Seed density, for example, tends to increase with percent soil moisture (Leckie et al. 2000) and decrease with pH (Pickett & McDonnell 1989).

Vegetation dynamics and seed banks are linked through disturbance (Jiménez & Armesto 1992). Effects of human disturbance on seed banks, especially fragmentation, are receiving increased attention. As landscapes become fragmented, distances generally increase between remnant patches and connecting corridors become eroded (Brothers & Spingarn 1992). The degree of separation and connectivity has important implications for seed dispersal (Primack & Miao 1992). As isolation and the intensity of land use increase, dispersal-restricted species such as ant, gravity, explosive, and wind dispersed species with heavy seeds, may become extirpated (McLachlan & Bazely 2001, Chapter 3). In contrast, many early successional and exotic plant species disperse effectively under these conditions (Stylinski & Allen 1999).

Seed banks surrounded by human-dominated landscapes often have increased proportions of introduced weedy species that have adapted to, or originated from similar conditions (Pickett & McDonnell 1989). Similarly, seed banks of disturbed forests often have comparatively lower seed densities (Ingersoll & Wilson 1990; Zabinski et al. 2000). As disturbance generally is positively associated with the presence of early successional species, the similarity of seed banks to aboveground vegetation consequently decreases (Qi & Scarratt 1998). Particularly intense disturbance may exclude some species characteristic of seed banks in undisturbed forests (Zabinski et al. 2000).

Few studies have examined the effects of disturbance on riparian forests, despite the important role they play in river ecosystem structure and function (Gregory et al. 1991; Tabacchi et al. 1998; Brinson & Ver Hoeven 1999). In cities, these forests often represent the only remaining natural green-space (Airola & Buchholz 1984), and in North America they are increasingly threatened by human use (Knutson & Klaas 1998). Though degraded by urban and agricultural land use, seed banks of riparian forests in Southern Manitoba have yet to be characterized. The overall objective of this study was to describe the seed bank of riparian forests along the Assiniboine River and its response to surrounding land use along an urban – rural gradient.

I predicted that the proportion of short-lived and exotic species in the seed bank would increase with disturbance, whereas species diversity and seed density would decrease. Further, effects of disturbance would be greatest in urban and least in low-intensity rural forest sites

## 4.2 Methods

### SITE DESCRIPTION

This study was conducted on 25 fragments of riparian forest along the Assiniboine River in southern Manitoba (Fig. 2.1, Appendix 1). The eastern-most forest patch (49°53'N, 97°08'W) was located at the junction of the Assiniboine River with the Red River in downtown Winnipeg, whereas the western most forest patch (50°02'N, 97°50'W) was approximately 50 km west, located north of the town of St. Eustache. 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 habitats in this region include 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 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 1998). The mean annual precipitation is 504.4 mm; 404.4 mm falls as rain, which peaks in June, while 100 mm water equivalent of snow falls annually.

### SAMPLING DESIGN

#### Site Level

Potential forest sites were identified along an urban-rural land use gradient using aerial photos taken in August 1991 and 1994 (Linnet Geomatics International Inc. 1998). Sites were classified according to surrounding land use and include: i) urban sites (U) in the downtown core characterized by high rise office and apartment buildings (Fig 3.1a); ii) suburban sites (S) located outside the downtown core, but within the city perimeter, characterized by single family dwellings (Fig 3.1b); iii) high intensity rural sites (H) surrounded by cash crops subject to regular pesticide and fertilizer use (Fig 3.1c); iv) low intensity rural sites (L) surrounded by forage crops not subject to pesticide and fertilizer use (Fig 3.1d); and v) reference sites (R) that are large, and are generally recognized as being relatively undisturbed. Once selected, each site was visited to ensure the remnant patch still existed as depicted in the aerial photos and to confirm classification.

At each site, three line transects were randomly located perpendicular to the river, and at least 20 m apart and 50 m distance from any parallel forest edge. If the forest patch was wider than 250 m, then one transect was randomly located in each of three evenly divided sections. Along each transect, sample points were permanently marked at 0, 15, and 50 m from both the land and river margins of the forest patch. The 0 m mark for the land margin in each site was located at the point of edge maintenance, or treated as a canopy drip line edge (Ranney et al. 1981). To eliminate the confounding effects of annual flooding, the 0 m mark on the river margin was located at the high-water line.

At each sample point, the species composition of herbs, defined as all herbaceous species and any woody plants less than 0.5 m in height, was recorded as percent cover from July 1 – August 31, 1999. Early flowering species were later identified from May 15 – July 15, 2000. Two 2 x 1 m quadrats per sample point were situated along each transect whereas one of the three transects was randomly selected for an additional third quadrat, resulting in 42 quadrats per site.

At each point, I measured forest canopy cover, calculated by averaging values visually assessed from the four corners of each 2 x 1 m quadrat, topography, classified on a scale that ranged from flat (1) to ridge and swale (4), and aspect. In addition, edaphic variables were measured at each sample point along the two transects without the third quadrat. Percent soil moisture was calculated using soil cores (4 x 20 cm) that were immediately weighed for wet mass and later oven-dried at 50°C for 24 hours in order 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 composition of percent sand, silt, and clay 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 et al. 1995). Peripheral and central selection was used to retain the maximum original variation of the soils, while ensuring that each of the 25 sites was represented. Soil composition of the reference samples was measured using the Bouycous Hydrometer Method (Karla & Maynard 1991).

Seed bank sampling occurred in conjunction with the vegetation sampling from July 1 – August 31, 1999. Along the two transects without the additional quadrat I collected a (10 x 15 x 10 cm deep) soil sample at each sampling point, excluding the point 50 m from the river edge. This resulted in a total soil surface area of 0.015 $m^2$ per sample point and 0.18 $m^2$ per site, whereas the 5 urban sites, which were too small to permit 50 m sample points, only resulted in 0.15 $m^2$ per site. 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 mixed with 200 ml of sterile growth medium (Sunshine Mix 4), to help break up the sample. Samples were then placed in 9.5 x 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. The number and identity of emergent seedlings was recorded to species using floras by Royer and Dickinson (1999) and Looman and Best (1987). Unidentified seedlings were transplanted and grown to maturity for identification. When seedlings were no longer emerging, the flats were stratified in a cold chamber at 2-3°C with a 12-hour photoperiod, for six weeks. When they were returned to the greenhouse the soil was broken up and stirred to encourage germination of buried seeds. Cold stratification was conducted twice at which point emergence had ceased after a total of 14 months in the greenhouse, and the project was terminated. Although the seedling emergence method may not meet the requirements for all species, it is the most accurate and efficient method to estimate community-scale seed bank composition (Gross 1990; Brown 1992).

### Landscape Level

Using aerial photographs, land use was digitized around each site using vector themes in ArcView 3.2. Land use was classified as urban (U), suburban (S), high intensity rural

(H), and low intensity rural (L) land use as defined above. In addition, healthy forest, degraded forest, and river were also classified. Healthy forest was defined as any portion of a patch having a minimum dimension greater than 30 m and without a manicured or mown understorey. Degraded forest was defined as any portion of a patch with a minimum dimension between 10 m and 30 m, without a manicured understorey. Any forest patches with a manicured understorey were classified according to contiguous land use. My land use classification was cross-referenced against classified 30 x 30 m LANDSAT imagery obtained from the Prairie Farm Rehabilitation Association (Agriculture & Agrifood Canada 1994, unpubl.). Any discrepancies between the two data sets were resolved using site visits and records of land use obtained from local landowners.

Proportions of each land use surrounding forest sites were measured within a 1000 m radius. A measure of connectivity, modified from Kenkel (1990), was calculated (Connectivity = $\Sigma A_i^2 (P_i D_i^2)^{-1}$, where A = patch area, P = perimeter, and D = center to center inter-patch distances) in order to assess the degree of isolation. Area:perimeter was calculated in order to assess shape in relation to fragmentation. Disturbance was calculated for each site as a categorical variable, and ranged from no disturbance (1) to highly disturbed (10). Starting from 1 it was calculated using the 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 site (0 or 1) and the interior of the site (0 or 1).

## ANALYTICAL METHODS

I analyzed the seed bank at two different levels of organization: the riparian forest as a whole, and site-level responses to the urban-rural land use gradient. To characterize the seed bank at each site, Hill's (1973) diversity measures $N_0$, which examines 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 which looks at $N_2$ divided by the total number of species, were used. In addition, seed density (seedlings$\cdot$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 calculating Soerenson's Similarity (SS), among sample points within each site for each land use category, and between each land use and reference land use ($SS = 2a\cdot(2a+b+c)^{-1}$, 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 1988). Post-hoc Tukey's tests ($\alpha = 0.05$) were used to separate means when overall treatment effects had been found significant.

The effect of land use on species in the seed bank was analyzed using a one-way ANOVA (SAS Institute 1988) again using Tukey's test, with emphasis on the 15 most frequent species (those that occurred in more than 5% of the pots). These species also were classified to functional groups. Functional groups included origin (native or exotic), life form (annual or perennial grass; annual, biennial, or perennial forb; or woody), phenology (ephemeral, summer, or fall flowering within March-May, June-August, or September-November, respectively), and dispersal mechanism (anemochore, barochore, autochore, epizoochore, endozoochore, or myrmecochore), which were categorized using Britton and Brown (1970) and Ridley (1930).

Canonical correspondence analysis (CCA), using Canoco version 3.11 (Ter Braak 1990), was conducted to determine relationships between species composition, site, and the constraining disturbance (Appendix 3) and environmental (Appendix 4) variables for the seed bank. Urban (U), suburban (S), high intensity rural (H), low intensity rural (L), and reference (R) land uses were classified as categorical variables and also used to constrain the seed bank species. CCA is a method of direct gradient analysis, which explains data through orthogonal axes of variation in decreasing order of importance. Correlations between species and environment variables are only meaningful if the redundancy value, the proportion of the total variance from the correspondence analysis that is explained when constrained by the environment variables, is sufficiently high. Rare species were always down-weighted in importance. Considering Oksanen and Minchin's (1997) discussion of stricter convergence criteria, which is missing in Canoco version 3.11, results from the ordination were confirmed with those generated by Podani's Syntax 5.0 (Podani 1994), which uses a more stable algorithm and is not susceptible to changes from data input order.

## 4.3 Results

### RIPARIAN FOREST SEED BANK

A total of 1565 seedlings emerged, representing 90 distinct taxa. Only 27 of these seedlings remained unidentified, most of which were biennials that never grew beyond the basal rosette stage. All taxa were identified to species except five that were only identified to genus and seven that remained unidentified. Species richness would have been higher; however, all *Carex* seedlings were lumped as *Carex* spp. as they rarely flower in greenhouses. 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 seedlings$\cdot$m$^{-2}$. Overall the richness of exotic and native species was nearly equal, although the density of exotic species was 2.3x that of native species.

Species composition of the riparian forest seed bank was significantly related to disturbance and environmental variables (Fig. 4.1). 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. These correlations were meaningful, as the redundancy value was very high at 54.6 % (Økland 1999).

Axis 1 was positively correlated with garbage and disturbance, and negatively correlated with area:perimeter, connectivity and percent soil moisture (Fig. 4.1b). Species positively associated with axis 1 were generally exotic or weedy (Fig. 4.1a). Although many of these were only found at one site or pot, the exotic species *Arctium minus*, and

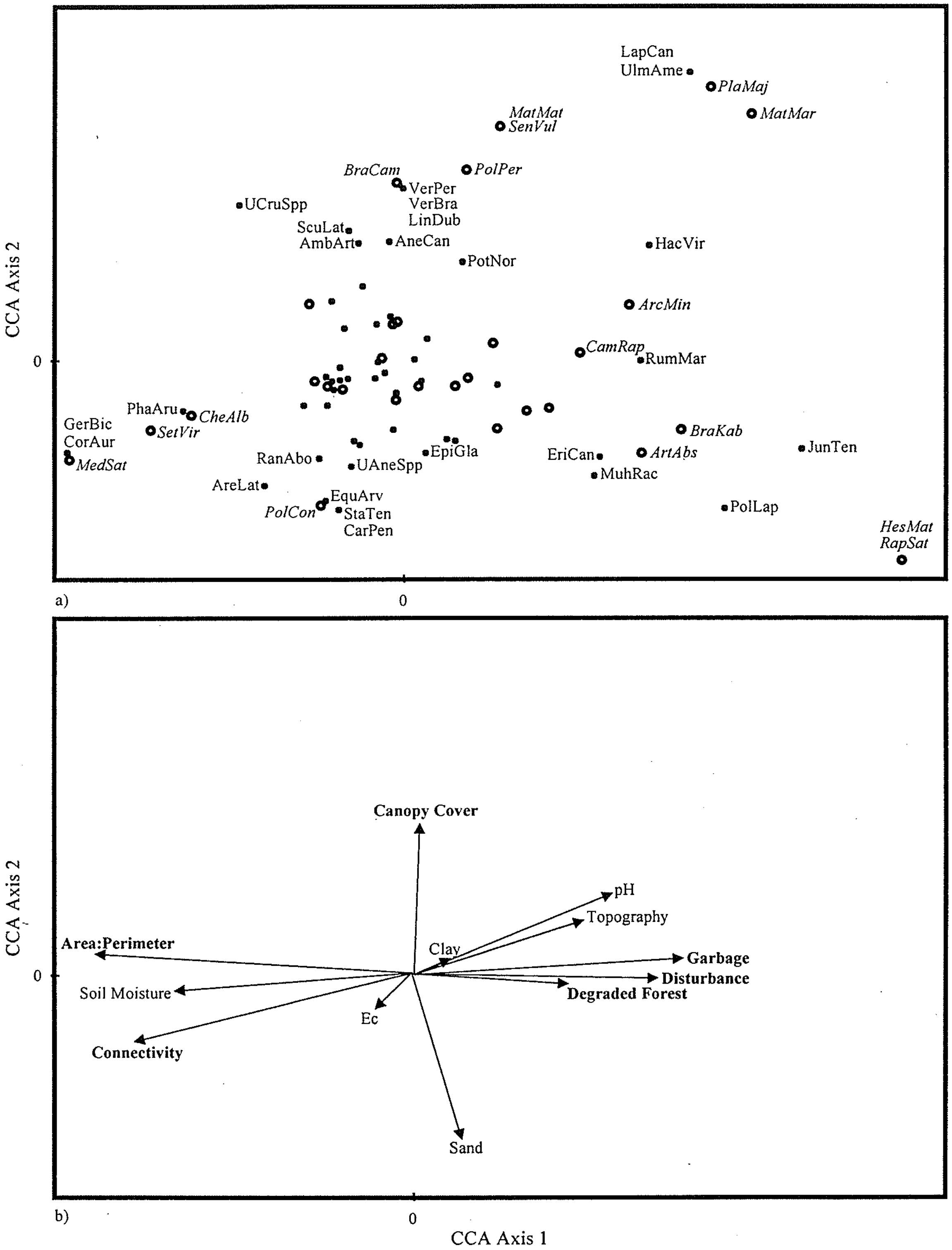


**Fig. 4.1**. Results of Canonical Correspondence Analysis (CCA) of riparian forest seed bank composition, constrained by environment and disturbance (bold face) variables. (a) N=84 species with selected exotic (open circle, italicized) and native (closed box) species depicted, full names in Appendix 2. (b) N=12 variables shown on 2x scale.

*Artemisia absinthe* were found in three and ten sites, respectively, and the weedy native species *Hackelia virginiana* was found in eight sites. Species negatively associated with axis 1 were generally interior or hydrophilic species. These, again, were infrequent, with the exception of *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 (Fig. 4.1b). These correlations were not as strong as those of axis 1 and species associated with axis 2 were generally infrequent. More common species positively associated with axis 2 included *Polygonum persicaria* and *Anemone canadensis*, whereas those negatively associated with axis 2 included *Epilobium glandulosum* and *Ranunculus abortivus* (Fig. 4.1a).

## SEED BANK RESPONSE TO LAND USE

Land use surrounding riparian forest had a substantial impact on the seed bank. Species richness was significantly ($P < 0.05$) lowest for urban and highest for low intensity rural sites, whereas the proportion of exotic to native diversity was significantly ($P < 0.05$) highest for urban sites (Table 4.1). The similarity between urban and reference sites was significantly lower ($P < 0.01$) than that for rural sites, and the seedling density of urban seed banks tended to be approximately half that of low intensity rural sites. (Table 4.1).

Land use was related to seed bank species composition. The 25 sites were grouped around their respective centroids when constrained by land use classification (Fig. 4.2a). 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

**Table 4.1**. Seed bank response to landuse (n=5) according to; Hill's diversity; species richness ($N_0$) and dominant species ($N_2$), eveness ($E_3$) density, exotic:native, and Sorenson's similarity; between seedbank and aboveground vegetation, within site seed bank composition, and between land use categories and reference sites.

| | | Land use category | | | | | ANOVA |
|---|---|---|---|---|---|---|---|
| | | Urban | Suburban | High rural | Low rural | Reference | *P* † |
| Seed Bank Diversity | | | | | | | |
| | $N_0$ | 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 |
| | $E_3$ | 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 |
| Sorenson 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 |

† NS, not significant ($P > 0.05$).

correspondence analysis. When constrained, the species-environment correlations were 0.953 and 0.875 for axes 1 and 2, respectively. These correlations again were meaningful, although they exhibited a lower redundancy value (26.9 %) than for the relationship between species composition and disturbance and environmental variables described above.

In general, most of the species unique to the categories of land use were infrequently found and, in most cases only occurred in one seed pot, although urban, low rural, and reference sites had unique species occurring in more than one seed pot or site. The five urban sites were clearly separated from the remaining 20 sites along axis 1, and were characterized by six unique exotic and three unique native species (Fig. 4.2). Of these, only the exotics *Hesperis matronalis* and *Plantago major* occurred in more than one pot. Sites from the four remaining land uses separated less clearly along axis 2 (Fig. 4.2a). Species unique to these four land uses that occurred in more than one pot were native *Phalaris arundinacea,* which was associated with reference sites, and natives *Ambrosia artemisiifolia, Ribes americanum, Scutellaria lateriflora,* and *Veronica peregrina,* which all were associated with low intensity rural sites.

Effects of land use also were examined for individual species (Table 4.2). Exotic *Hackelia virginiana* was significantly ($P = 0.041$) associated with urban sites, exotic *Poa pratensis* significantly ($P < 0.0001$) associated with suburban sites, and exotic *Thlaspi arvense* significantly ($P = 0.010$) associated with low intensity rural sites. In contrast, native species *Anemone canadensis* ($P < 0.0005$), *Carex* spp ($P = 0.004$), *Rubus idaeus* ($P = 0.014$), and *Galium triflorum* ($P = 0.021$) were significantly absent from urban sites (Table 4.2).

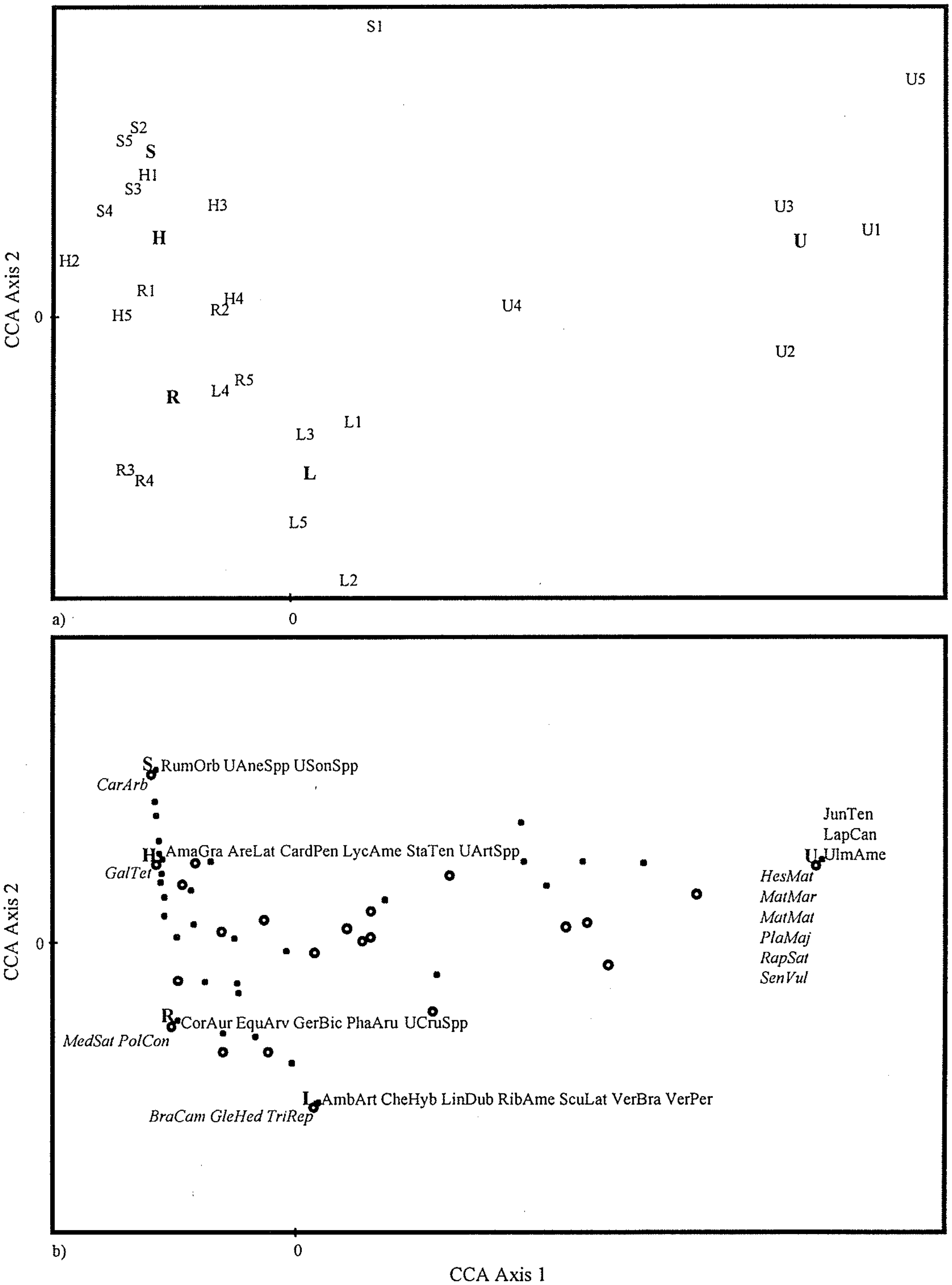


**Fig. 4.2.** Results of Canonical Correspondence Analysis (CCA) of riparian forest seed bank, constrained by land use class with the centroid (bold face) shown for (a) N=25 sites and (b) N=84 species with selected exotic (open circle, italicized) and native (closed box) species depicted, full names in Appendix 2. Land use classes are urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R).

**Table 4.2.** Characterization of the 15 most frequent (occurring in > 5% of the pots) riparian forest seed bank species, with mean densities (N=5, seedlings / $m^2$) for each land use. ANOVA with Tukey's test analyzed using Log density.

| Species | Rank | Origin | Life Form | Phenology | Dispersal Type | Land use categories | | | | | ANOVA $P$ † |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Urban | Suburban | High rural | Low rural | Reference | |
| *Poa pratense* | 1 | E | PG | S | END | 6.7 c | 168.0 a | 85.3 ab | 20.0 bc | 28.0 abc | 0.003 |
| *Sonchus arvensis* | 2 | E | PF | F | ANE | 13.3 | 24.0 | 33.3 | 17.3 | 25.3 | NS |
| *Cirsium arvense* | 3 | E | PF | F | ANE | 21.7 | 12.0 | 33.3 | 36.0 | 28.0 | NS |
| *Carex* Spp. ‡ | 4 | N | PG | S | BAR | 0.0 b | 32.0 ab | 78.7 a | 36.0 ab | 30.7 a | 0.0041 |
| *Potentilla norvegica* | 5 | N | AF | F | END | 31.7 | 6.7 | 4.0 | 36.0 | 8.0 | NS |
| *Taraxicum officinale* | 6 | E | PF | E | ANE | 11.7 | 12.0 | 5.3 | 21.3 | 2.7 | NS |
| *Urtica dioica* | 7 | E | PF | F | END | 33.3 | 4.0 | 70.7 | 50.7 | 1.3 | NS |
| *Galium triflorum* | 8 | N | PF | S | END | 0.0 a | 0.0 a | 13.3 a | 49.3 a | 12.0 a | 0.0206 |
| *Rubus idaeus* | 9 | N | W | E | END | 0.0 b | 4.0 ab | 17.3 ab | 28.0 a | 5.3 ab | 0.0138 |
| *Plantago media* | 10 | E | PF | F | END | 1.7 | 9.3 | 10.7 | 8.0 | 12.0 | NS |
| *Thlaspi arvense* | 11 | E | AF | S | ANE | 3.3 b | 5.3 ab | 1.3 b | 133.3 a | 86.7 ab | 0.0098 |
| *Oxalis europaea* | 12 | N | PF | S | AUT | 3.3 | 8.0 | 4.0 | 12.0 | 5.3 | NS |
| *Anemone canadensis* | 13 | N | PF | S | ANE | 0.0 b | 4.0 b | 1.3 b | 65.3 a | 1.3 b | 0.0005 |
| *Artemisia absinthium* | 14 | E | PF | F | ANE | 48.3 | 1.3 | 1.3 | 5.3 | 10.7 | NS |
| *Hackelia virginiana* | 15 | N | BF | S | EPI | 23.3 a | 9.3 ab | 1.3 ab | 2.7 ab | 0.0 b | 0.0409 |

† NS, not significant ($P > 0.05$).

‡ Includes all *Carex* not identified to species.

## 4.4 Discussion

### RIPARIAN FOREST SEED BANK

The mean density of the seed bank for the riparian forest in my study area was comparable to those found for a temperate forest in Japan (Nakagoshi, 1985) and for riparian forests in northern Sweden (Grelsson & Nilsson 1991), although the range exhibited in my study was much lower. Whereas others have found sites with no seed bank (e.g., Matlack & Good 1990; Grelsson & Nilsson 1991), sites in my study area always contained seeds, likely because of the high proportion of exotic species, which produce many long-lived seeds. The upper value of my seed bank density range, however, was lower than those of other studies, perhaps, in part, because all of my forest sites were somewhat degraded in response to surrounding land use. In turn, this range in land use is related to the high diversity exhibited in my study. These seed banks contained 50 % more species than those of a coastal plain forest in New Jersey (Matlack & Good 1990) and an Allegheny Plateau riparian forest in Pennsylvania (Hanlon et al. 1998).

The seed bank in my study was dominated by exotic species. Relative to other riparian forests (e.g., Hanlon et al. 1998), the proportion of herbaceous and exotic species was larger, and that of woody and perennial species smaller. This, again, is likely in response to the degradation exhibited by these sites. Ephemeral species were rare in this seed bank, reflecting their relative absence from the aboveground vegetation (Chapter 3). This may be a response to the northern location of my study site, ostensibly, at the edge of distribution for many of these species, but may also reflect their relative vulnerability of ephemerals to disturbance (McLachlan & Bazely, 2001) and the decline in these forests associated with surrounding land use.

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 with a large amount of garbage exhibited the greatest number of exotic and ruderal species. As human use increases and habitat becomes more open, sites become more susceptible to invasion, and seed banks exhibit an increase in the proportion of exotics (Zabinski et al. 2000). Although my sites were often degraded and I expected mostly shade-intolerant species, a large number of shade-tolerant forest species remained in the seed bank. For example, the fourth most frequent taxum was *Carex* spp., which are typically abundant in forest seed banks (Pickett & McDonnell 1989; Matlack & Good 1990). In other studies, even those of relatively undisturbed sites, seed banks are also rich in both shade tolerant and intolerant species (e.g., Leckie et al. 2000).

## LAND USE

In my study, land use had a substantial impact on the riparian forests along the urban to rural gradient. Urban land use had the greatest effect on species composition, diversity, and density of the seed bank. Although the effects of suburban land use were not as severe as those of urban use, they too altered the species composition and diversity and seed density. This response to use-associated disturbance was similarly, but more strongly, reflected by aboveground herbaceous species (Chapter 3). In urban sites, both seed banks and aboveground vegetation exhibited higher exotic:native ratios, as these sites were much more disturbed, dominated by edge habitat, had little if any interior, and consisted of secondary forest. Urban seed banks were dominated by exotic and ruderal 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 apparent lower seed density of urban sites may also be a response to the condition of these sites. The isolation and small size of urban sites has likely decreased the seed input from surrounding natural habitat. In addition, it is likely that few of the seeds dispersing into urban sites become entrapped due to their typically compacted (Zabinski et al. 2000) and drier soils (Leckie et. al. 2000).

Disturbance associated with urban land use was intense enough to eliminate broad groups of species from both the seed bank and the above ground vegetation. Indeed, four of the most dominant native species, including *Anemone canadensis* and *Carex* spp, had been eliminated from urban seed banks. Although moderate disturbance (here associated with suburban and rural land use) altered the community composition, it seems to replace rare with more common species (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 et al. 2000). This is especially true of human disturbance, as many Eurasian exotics have evolved in response to human land use (Forcella & Harvey 1983). The establishment of competitive exotic species may, in turn, prevent the regeneration of native species (Stylinski & Allen 1999).

In contrast to the aboveground vegetation, no relationship to an edge to interior site level gradient was exhibited by the seed bank. My 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. Additional effects of downriver cumulative "disturbance loading", whether as siltation, nutrient concentration, or pesticide concentration, may have further contributed to variation among sites and warrants future investigation. Although seed banks in this study did show a substantial response to land use, my approach was correlative and actual difference in seed dispersal among sites should be investigated in the future.

## CONCLUSION

This study significantly contributes to an understanding of the impacts of human disturbance on riparian forest seed banks, and is the first of its kind in Manitoba. I have shown that urban land use has had the greatest effect on riparian forest seed banks, and the introduction of exotics was associated with changes in native species composition and declines in species diversity and seed density.

These results represent an important first step for the management of riparian forests as it has generated much needed information regarding the impacts of land use. The loss of some species and the decline in seed density and species diversity associated with increased disturbance from land use suggests that regeneration from the seed bank would lead to a shift in the species composition. In particular, urban sites, with their very low diversity and density and the high proportion of exotic species, cannot rely solely on the seed bank for future regeneration. Recovery of these sites in the future will likely depend on active management including the removal of exotics and the planting of native species. It is, thus, important to understand how disturbance affects seed banks when planning effective conservation and restoration strategies for riparian forests in human dominated landscapes.

# CHAPTER 5: Understorey indicators of disturbance for riparian forests along an urban-rural gradient in Manitoba.

## 5.1 Introduction

In light of the extensive landscape modification and disturbance associated with human land use, it is critical that I effectively identify and monitor associated changes in these systems. The role of disturbance is generally recognized as fundamental in determining plant communities. It can be defined as any event that alters the composition and structure of ecosystems, communities, or populations associated with changes in the historical range of variation in resource availability and/or physical environment (Godron & Formann 1983). Although ecological research traditionally has focused on natural disturbance, anthropogenic sources are receiving increasing attention. Of these, fragmentation, and its combined effects of habitat loss and isolation, has been described as one of the greatest threats to and causes of species extinction (Wilcox & Murphy 1985).

Reductions in forest area are generally associated with declines in plant diversity (Airola & Buchholz 1984; Vogelmann 1995) and proportional increases in edge habitat (Saunders et al. 1991). The latter increases the susceptibility of forests to establishment by xeric and shade intolerant species as well as invasion by exotic species (Brothers & Spingarn 1992). In turn, isolation has important implications for plant-related processes including colonization and seed dispersal (Primack & Miao 1992). As isolation increases, dispersal-restricted species (ie. those that are ant, gravity, and explosive dispersed) may become extirpated (Dzwonko & Loster 1992). In contrast, early successional and exotic plant species tend to be effective dispersers under these conditions (Stylinski & Allen 1999).

Over the last century, landscapes across central North America have become fragmented by agricultural use, with a consequent shift in land cover from prairies and late-successional forests dominated by perennial native species to those that are relatively homogenous and dominated by annual crops and weed species (Delong & Brusven 1998). In turn, these landscapes have been increasingly converted to urban land use, and exhibited a sharp decline in vegetation cover (McDonnell & Pickett 1990). This extensive landscape modification has lead to a complex urban-rural gradient, which can be viewed as an extension of the gradient paradigm (*sensu* R. Whittaker 1967).

Urban development decreases patch size within cities and increases isolation among urban and rural remnant patches (Davis & Glick 1978). Typically, extant urban forest is severely disturbed, and exhibits compacted soils, and declines in both overstorey canopy cover (Airola & Buchholz 1984) and native understorey species diversity (Cole & Marion 1988; Kuss & Hall 1991; Drayton & Primack 1996), and increases in exotic and ruderal species diversity (Rudnicky & McDonnell 1989; Freedman et al. 1996; Chapter 3). Because of the scale and complexity of these effects, indicators are increasingly used to monitor and mitigate these changes.

Indicators are any discrete feature of the environment that reflect the condition of the surrounding ecosystem and can provide a quantitative measure of ecological resources (Schiller et al. 2001). To be effectively used as indicators, species should be adequately common and understood, and sensitive to underlying changes in the biophysical environment (Angelstam 1998). Understorey herbs have been successfully used as indicators of; deciduous forest regeneration in southern Canada (McLachlan & Bazely 2001), long-term continuity of boreal forests in Sweden (Ohlson et al. 1997), and riparian forest disturbance in southern U.S.A. (Bratton et al. 1994).

Plants are often used as indicators in order to eliminate the need for a full description of the understorey, which may be too fine in scale and resource-intensive to complete. Although diversity measures, such as total species richness, are often employed, they have been criticized as being too coarse, insensitive to underlying changes in species composition, and of questionable use in predicting future change (Lawton et al. 1998). The use of guilds, groups of species that are functionally related and have similar resource requirements (Root 1967), may represent an intermediate solution for describing the impacts of disturbance (Hobbs 1997). For example, bird habitat assemblages were significantly related to forest condition in a study of anthropogenic disturbance (Canterbury et al. 2000). Life form has been used to monitor forest disturbance (McIntyre et al. 1995) whereas origin and habitat preference were related to species loss and compositional change associated with urban land use (Drayton & Primack 1996). Flowering phenology and seed dispersal guilds were significantly related to species decline associated with human use (McLachlan & Bazely 2001).

My overall objective was to identify effective indicators of riparian forest degradation associated with land use along an urban-rural gradient in Southern Manitoba. More specifically I wanted to: 1) identify species that exhibited significant relationships with changes in environment and disturbance associated with land use; 2) identify functional characteristics that underlay species-level response to land use; and 3) identify species that were good indicators of changes in species diversity associated with land use.

I predicted that effective indicators of disturbance would tend to be associated with urban land use, be exotic, have annual life forms, and be unrestricted in their seed dispersal. In contrast, effective indicators of high integrity habitat will be associated with reference sites, be native, have perennial life histories, ephemeral flowering, and be dispersal-restricted.

## 5.2 Methods

### SITE DESCRIPTION

This study was conducted on 25 fragments of riparian forest along the Assiniboine River in southern Manitoba (Fig. 2.1, Appendix 1). The eastern-most forest patch (49°53'N, 97°08'W) was located at the junction of the Assiniboine River with the Red River in downtown Winnipeg, whereas the western-most (50°02'N, 97°50'W) was approximately 50 km west, located north of the town of St. Eustache. The study area was located at the southeast portion of the prairie ecozone, where agriculture currently represents 94 % of the land base (Wiken 1996). Remnant natural habitat in this region is dominated by 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 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 1998). Mean annual precipitation is 504.4 mm; 404.4 mm falls as rain, which peaks in June, while 100 mm water equivalent of snow falls annually.

### SAMPLING DESIGN

#### Site Level

Potential forest sites were identified along an urban-rural land use gradient using aerial photos taken 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 (Fig. 3.1a); ii) suburban sites located outside the downtown core, but within the city perimeter, characterized by single family dwellings (Fig. 3.1b); iii) high-intensity rural sites surrounded by cash crops subject to regular pesticide and fertilizer use (Fig 3.1c); iv) low-intensity rural sites surrounded by forage crops not subject to pesticide and fertilizer use (Fig 3.1d); and v) reference sites that are relatively large, and are generally recognized as being high in quality. Once selected, each site was visited to ensure the remnant patch still existed as depicted in the aerial photos and to confirm classification.

At each site, three line transects were randomly located perpendicular to the river, and at least 20 m apart and 50 m distance from any parallel forest edge. If the forest patch was wider than 250 m, then one transect was randomly located in each of three evenly divided sections. Along each transect, sample points were permanently marked at 0, 15, and 50 m from both the land and river edges of the forest patch. The 0 m mark for the land edge in each site was either located at the point of edge maintenance or treated as a canopy drip line edge (Ranney et al. 1981). To eliminate the confounding effects of 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 all herbaceous species and any woody plants less than 0.5 m in height, was identified (nomenclature follows Looman & Best 1987) and recorded as percent cover from July 1 – August 31, 1999. Early flowering species were later identified from May 15 – July 15, 2000. Two 2 x 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, resulting in 42 quadrats per site.

At each sample point, I measured forest canopy cover, calculated by averaging values visually assessed from the four corners of each 2 x 1 m quadrat, and topography, classified on a scale that ranged from flat (1) to ridge and swale (4). In addition, edaphic variables were measured at each sample point along the two transects without the third quadrat. Percent soil moisture was calculated using soil cores (4 x 20 cm) that were immediately weighed for wet mass and later oven-dried at 50°C for 24 hours in order 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 composition 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 et al. 1995). Peripheral and central selection was used to retain the maximum original variation of the soils, while ensuring that each of the 25 sites was represented. Soil composition of the reference samples was measured using the Bouycous Hydrometer Method (Karla & Maynard 1991).

### Landscape Level

Using aerial photographs, land use was digitized around each site using vector themes in ArcView 3.2. Land use was classified 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 understorey. Degraded forest was defined as any portion of a patch with a minimum dimension between 10 m and 30 m, without a manicured understorey. Any forest patches with a manicured understorey were classified according to contiguous land use. My land use classification was cross-referenced against classified 30 x 30 m LANDSAT imagery obtained from the Prairie Farm Rehabilitation Association (Agriculture & Agrifood Canada 1994, unpubl.). Any discrepancies between these two data sets were resolved using site visits and records of land use obtained from landowners.

Proportions of each land use surrounding forest sites were measured within a 1000 m radius. Area:perimeter was calculated in order to assess shape in relation to fragmentation. A measure of connectivity (modified from Kenkel 1990) was calculated (Connectivity = $\Sigma A_i^2 (P_i D_i^2)^{-1}$, where A = patch area, P = perimeter, and D = center to center inter-patch distances) in order to assess the degree of isolation. Intensity of disturbance was described for each site as a categorical variable, and ranged from no disturbance to highly disturbed. Starting from 1 it was calculated using the 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 site (0 or 1), and the interior of the site (0 or 1).

## ANALYTICAL METHODS

Only species that occurred in two or more sites of any land use category were analyzed. Percent cover data were averaged for individual species to give mean species cover for each of the 25 sites. The proportional occurrence of individual species also was calculated for each site and used for subsequent analysis as, unlike mean cover, differences in abundance are unaffected by organism size. Data were log transformed, to meet the assumptions of normality (Zar 1996), and untransformed data are presented.

Effects of land use on plant species composition were analyzed using cluster analysis, with minimum increase in error sum of squares and euclidean distance (Podani 1994). Effects of land use on plant species occurrence were analyzed using one-way analysis of variance (ANOVA) (SAS Institute 1988). Effects of land use on species occurrence and diversity were also conducted using one-way ANOVA for city (combined urban and suburban sites) and non-city use (combined low-intensity rural, high-intensity rural, and reference sites). Because of the large number (N = 127) of tested species, a more conservative significance level, $p < 0.005$, was used. Post-hoc Tukey's tests ($\alpha = 0.05$) were used to separate means when overall treatment effects had been found significant.

The relationship of species occurrence with disturbance (Appendix 3) and environmental (Appendix 4) variables was analyzed using multiple regression (SAS Institute 1988). Averaged for each of the 25 sites, disturbance variables include connectivity, area:perimeter, garbage levels, intensity of disturbance, canopy cover, and the proportion of degraded forest, whereas environmental variables include percent soil moisture, pH, Ec, topography, and percent sand and clay. Proportion of healthy forest and site area were subsequently eliminated because of their high correlation ($r > 0.90$) with connectivity and area: perimeter, respectively, and percent silt was eliminated as it was derived from percent sand and clay.

In order to develop a list of potential indicator species vulnerability and opportunism were examined. Vulnerability was defined as the proportion of reference sites (N = 5) within which a species occurred, divided by the proportion of city sites (N = 10) in which it occurred. In contrast, opportunism was defined as the proportion of city sites (N = 10) within which a species occurred, divided by the proportion of non-city sites (N = 15) in which it occurred. A ratio of vulnerability index (VI) over opportunist index (OI) was calculated, indicating the likelihood that a species would be affected by land use. Species more likely to occur in reference sites, thus having a ratio value > 1, were divided into four response categories according to the clustering of data. Categories included species that were excluded from city sites, with a ratio value of infinity (VI1); species that were much more common in reference sites, with a ratio value > 5 (VI2); species that were more common in reference sites, with a ratio value between 2 and 5 (VI3); and species that were only slightly more common, with a ratio value between 1 and 2 (VI4). In turn, species that were more likely to occur in city sites, thus having a ratio value < 1, were divided into three response categories: species that were excluded from all non-city sites, with a ratio value approaching 0 (OI1); species that were more common in city sites and only excluded from reference sites, with a ratio value between 0.01 and 0.5 (OI2); and species that were only slightly more common in city sites, with a ratio value between 0.5 and 1. Species that were equally likely to be found in either city or non-city sites, having a ratio value of 1, were considered generalists.

Species were classified to guilds, which included origin (native or exotic), life form (annual or perennial grass; annual, biennial, or perennial forb; or woody), phenology (ephemeral, summer, or fall, that flowered from March-May, June-August, or September-November, respectively), and dispersal type (anemochore or wind-dispersed, barochore or gravity-dispersed, autochore or explosion-dispersed, epizoochore or animal carried, endozoochore or animal consumed, and myrmecochore or ant-dispersed), categorized using Britton and Brown (1970) and Ridley (1930). Vulnerability and opportunism ratio categories were characterized by using the proportion of species in each of these guilds.

Log-likelihood tests were conducted to assess the significance of the relationship between vulnerability or opportunism and these guilds.

Potential indicator species identified from all previous analyses of response to land use, relation to disturbance and environmental variables, and vulnerability or opportunistic classification (excluding VI3, VI4, OI3 and generalists) were further tested for their use as indicators using Pearson correlation of their proportional occurrence with diversity. $N_0$, which examines the total number of species but is sensitive to rare species, and $N_2$, which is the reciprocal of Simpson's index and emphasizes dominance, were calculated for exotic, native, and all species at each site (Hill 1973). In addition, $N_0$ was calculated for vulnerable (combined VI1 and VI2), and opportunistic (combined DI1 and DI2) categories of species.

## 5.3 Results

### COMMUNITY RESPONSE

The response of all understorey plant communities to land use was examined, and sites separated along the urban-rural gradient into urban, suburban, and rural groups (Fig. 5.1). Urban sites had the most distinct species composition and were most distant from the other groupings. Suburban sites formed the next grouping, were not as distant from the rural grouping, and included two non-suburban sites: R1, which was a reference site located in the suburban matrix, and H1, a high-intensity rural site that was within 500 m of the city boundary (Fig. 5.1). The third grouping, which was the least distinct, included high-intensity rural, low-intensity rural, and reference sites, all of which occurred within a rural matrix. Within this group, a subgroup including three of the reference sites appeared to separate out from the others.

### SPECIES RESPONSE

Eighteen of the 127 species occurring at least twice within any land use, differed significantly ($P$ □ 0.005) in proportional occurrence among land use categories (Table 5.1). There were four distinct land use responses among these species. A subset of species, "urban exploiters", was positively associated with urban land use and excluded from other land uses, and included the exotic *Chenopodium hybridum, Setaria viridis,* and *Solanum dulcamara.* Another subset of species, "urban avoiders", was negatively associated with urban land use and, largely absent from urban sites but occurred in all other land uses. They included the native *Amelanchier alnifolia*, which occurred most frequently in suburban sites, and *Carex* spp., which occurred most frequently in low-

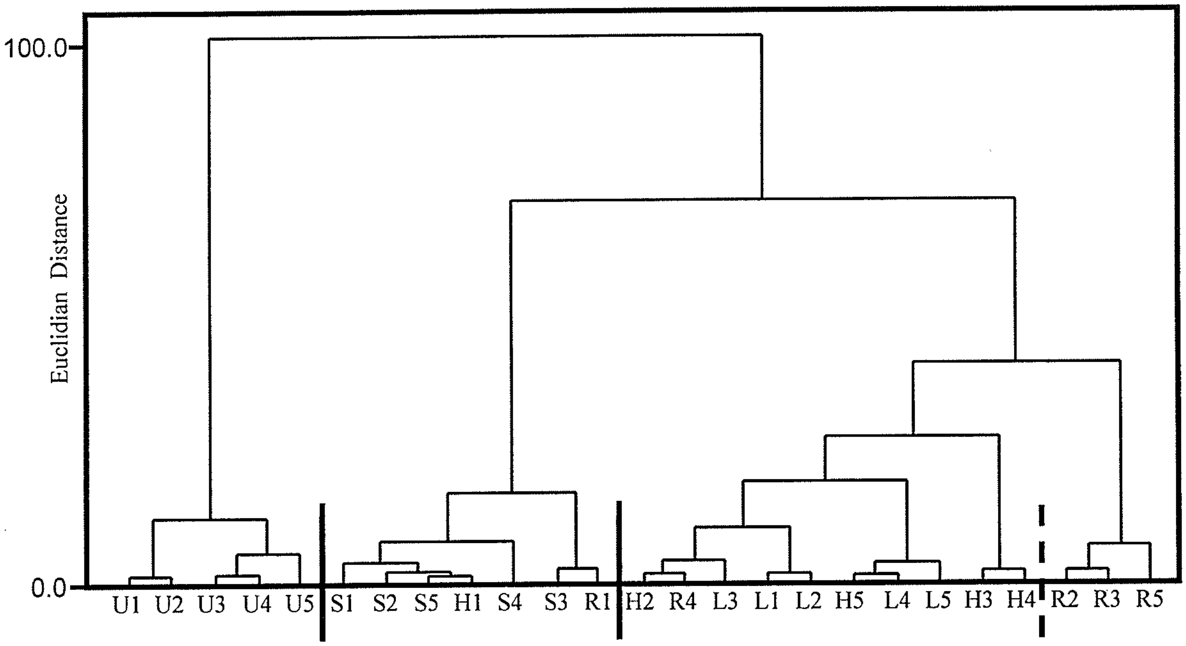


**Fig. 5.1**. Cluster analysis of the 25 study sites categorized to land use: U, urban; S, suburban; H, high-intensity rural; L, low-intensity rural; and R, reference. Sites were clustered according to species composition using Euclidean distance based on the minimum increase in error sum of squares clustering method.

**Table 5.1**. Summary of plant species showing a significant response to land use. Data are presented as mean proportional occurrence, separated using Tukey's HSD, and with *P* values from one-way ANOVAs of land use and of city vs. non-city†.

| | Land use category | | | | | | City vs. Non-city | | |
|---|---|---|---|---|---|---|---|---|---|
| Species‡ | Urban | Suburban | High rural | Low rural | Reference | *P* § | City | Non-city | *P* |
| *Amelanchier alnifolia* | 0.01 c | 0.44 a | 0.23 ab | 0.06 bc | 0.12 bc | < 0.0001 | 0.21 | 0.13 | NS |
| *Anemone canadensis* | 0.01 | 0.08 | 0.13 | 0.27 | 0.17 | NS | 0.04 b | 0.19 a | 0.0032 |
| ***Arctium minor*** | 0.43 a | 0.03 b | 0.12 b | 0.18 ab | 0.06 b | 0.0013 | 0.21 | 0.12 | NS |
| *Aster simplex* | 0.00 c | 0.01 c | 0.05 bc | 0.18 a | 0.15 ab | < 0.0001 | 0.00 b | 0.13 a | 0.0002 |
| *Carex* spp.# | 0.01 b | 0.45 a | 0.42 a | 0.36 a | 0.55 a | 0.0001 | 0.21 | 0.44 | NS |
| *Chenopodium hybridum* | 0.02 a | 0.00 b | 0.00 b | 0.00 b | 0.00 b | 0.0024 | 0.01 | 0.00 | NS |
| *Fraxinus pennsylvanica* | 0.33 | 0.41 | 0.64 | 0.66 | 0.56 | NS | 0.37 b | 0.62 a | 0.0005 |
| *Galium triflorum* | 0.00 b | 0.01 b | 0.31 a | 0.51 a | 0.35 a | < 0.0001 | 0.01 b | 0.39 a | < 0.0001 |
| *Lonicera dioica* | 0.00 b | 0.18 a | 0.02 b | 0.01 b | 0.05 b | 0.0005 | 0.09 | 0.03 | NS |
| ***Lonicera tartarica*** | 0.05 ab | 0.08 a | 0.01 bc | 0.00 c | 0.00 c | < 0.0001 | 0.06 a | 0.00 b | < 0.0001 |
| *Prunus virginiana* | 0.10 b | 0.44 a | 0.23 ab | 0.12 b | 0.11 b | 0.0019 | 0.26 | 0.15 | NS |
| ***Rhamnus cathartica*** | 0.23 ab | 0.51 a | 0.04 b | 0.01 b | 0.00 b | 0.0029 | 0.36 a | 0.02 b | 0.0003 |

**Table 5.1**. Continued.

| | Land use category | | | | | | City vs. Non-city | | |
|---|---|---|---|---|---|---|---|---|---|
| | Urban | Suburban | High rural | Low rural | Reference | *P* | City | Non-city | *P* |
| *Rubus idaeus* | 0.00 c | 0.01 bc | 0.12 ab | 0.22 b | 0.10 b | < 0.0001 | 0.01 b | 0.15 a | < 0.0001 |
| ***Setaria viridis*** | 0.02 a | 0.00 b | 0.00 b | 0.00 b | 0.00 b | 0.0024 | 0.01 | 0.00 | NS |
| *Smilax herbacea* | 0.01 b | 0.29 a | 0.49 a | 0.31 a | 0.33 a | < 0.0001 | 0.14 b | 0.38 a | 0.0019 |
| ***Solanum dulcamara*** | 0.28 a | 0.00 b | 0.00 b | 0.00 b | 0.00 b | 0.0005 | 0.13 | 0.00 | NS |
| ***Sonchus arvensis*** | 0.03 b | 0.14 ab | 0.19 ab | 0.33 a | 0.18 ab | 0.0027 | 0.08 b | 0.23 a | 0.0029 |
| *Stachys tenuifolia* | 0.01 b | 0.00 b | 0.12 a | 0.13 a | 0.10 a | 0.0005 | 0.00 b | 0.12 a | < 0.0001 |
| *Thalictrum venulosum* | 0.03 b | 0.30 a | 0.26 ab | 0.39 a | 0.37 a | 0.0016 | 0.16 | 0.34 | NS |
| *Viburnum rafinesquianum* | 0.02 b | 0.37 a | 0.10 b | 0.01 b | 0.13 b | 0.0003 | 0.18 | 0.08 | NS |

† City combines urban and suburban land uses, non-city combines high rural, low rural, and reference land uses.

‡ Bold faced species indicates exotic origin.

§ NS, not significant ( $P > 0.005$).

#All *Carex* species grouped together.

intensity rural sites. A third subset of species was positively associated with suburban land use and also occurred in urban sites, but was nearly absent from all rural sites. They included the exotics *Lonicera tartarica* and *Rhamnus cathartica.* A final subset of "non-city" species was positively associated with rural land use and was nearly absent from urban and suburban sites. They included the native *Aster simplex, Galium triflorum, Rubus idaeus,* and *Stachys tenuifolia* and all were most frequent in low-intensity rural sites.

When land use categories were further grouped to city (urban and suburban) and non-city (low rural, high rural, and reference) use, eight of the previously identified 18 species, and an additional two, showed a significant ($P < 0.005$) response to land use (Table 5.1). Of these, the exotic species *L. tartarica* and *R. cathartica*, were significantly more likely to occur in city sites. The only other exotic, *Sonchus arvensis*, had higher proportional occurrence in non-city sites, as did the seven native species. There also were significant differences in diversity between city and non-city sites. City sites had significantly lower native $N_0$ (ANOVA, $F_{1,24} = 9.74$, $P = 0.0048$), total $N_0$ (ANOVA, $F_{1,24} = 6.76$, $P = 0.016$), and native $N_2$ (ANOVA, $F_{1,24} = 7.14$, $P = 0.0136$), whereas they tended to have higher exotic $N_0$ and $N_2$.

Disturbance variables significantly ($P < 0.005$) predicted the occurrence of eight species. Intensity of disturbance and cover of garbage had the greatest effect on species occurrence, although all disturbance variables, except canopy cover, were significantly related to at least one species (Table 5.2a). Occurrences of the exotic *S. dulcamara* ($r^2 = 0.72$, df = 6,18, $P < 0.0001$) and *Urtica dioica* ($r^2 = 0.53$, df = 6,18, $P = 0.0021$), were significantly and positively associated with disturbance, and both increased with cover of

**Table 5.2.** Results of multiple regression testing the relationship of species proportional occurernce with the independent a) disturbance † and b) environmental ‡ variables.

| a) | | | Standardized ß for independent variable § | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species# | *P* | $r^2$ | AP | CanCov | Conn | DF | Dstrb | Grbg |
| *Carex* spp.†† | 0.0037 | 0.50 | 0.293 $^{NS}$ | 0.073 $^{NS}$ | 0.096 $^{NS}$ | 0.431 $^{*}$ | -0.066 $^{NS}$ | -0.610 $^{*}$ |
| *Galium triflorum* | 0.0011 | 0.57 | 0.094 $^{NS}$ | 0.118 $^{NS}$ | -0.079 $^{NS}$ | 0.050 $^{NS}$ | -0.929 $^{**}$ | 0.142 $^{NS}$ |
| *Phalaris arundinacea* | 0.0002 | 0.65 | 0.270 $^{NS}$ | -0.051 $^{NS}$ | 0.718 $^{**}$ | 0.222 $^{NS}$ | -0.231 $^{NS}$ | 0.212 $^{NS}$ |
| *Ranunculus abortivus* | 0.0009 | 0.58 | -0.809 $^{**}$ | -0.026 $^{NS}$ | 0.873 $^{***}$ | 0.032 $^{NS}$ | -0.855 $^{**}$ | 0.098 $^{NS}$ |
| *Rubus idaeus* | 0.0007 | 0.59 | 0.029 $^{NS}$ | -0.218 $^{NS}$ | -0.192 $^{NS}$ | -0.073 $^{NS}$ | -0.988 $^{***}$ | 0.323 $^{NS}$ |
| ***Solanum dulcamara*** | < 0.0001 | 0.72 | -0.002 $^{NS}$ | -0.186 $^{NS}$ | -0.062 $^{NS}$ | 0.038 $^{NS}$ | -0.301 $^{NS}$ | 1.000 $^{***}$ |
| *Symphoricarpos occidentalis* | 0.0030 | 0.51 | 0.136 $^{NS}$ | -0.284 $^{NS}$ | -0.076 $^{NS}$ | 0.044 $^{NS}$ | 0.777 $^{*}$ | -1.000 $^{***}$ |
| ***Urtica dioica*** | 0.0021 | 0.53 | -0.258 $^{NS}$ | 0.239 $^{NS}$ | 0.309 $^{NS}$ | 0.115 $^{NS}$ | -0.732 $^{*}$ | 1.000 $^{***}$ |

| b) | $P$ | $r^2$ | Clay | Ec | PSM | pH | Sand | Topo |
|---|---|---|---|---|---|---|---|---|
| *Actaea rubra* | 0.0038 | 0.50 | -0.068 $^{NS}$ | -0.133 $^{NS}$ | 0.689 $^{*}$ | 0.421 $^{NS}$ | 0.592 $^{*}$ | 0.018 $^{NS}$ |
| *Amelanchier alnifolia* | 0.0014 | 0.56 | 0.737 $^{*}$ | -0.358 $^{*}$ | 0.769 $^{**}$ | 0.313 $^{NS}$ | 0.876 $^{***}$ | -0.200 $^{NS}$ |
| *Crataegus crysocarpa* | 0.0019 | 0.54 | 0.255 $^{NS}$ | -0.275 $^{NS}$ | -0.210 $^{NS}$ | -0.755 $^{*}$ | 0.045 $^{NS}$ | -0.189 $^{NS}$ |
| *Galium boreale* | 0.0001 | 0.64 | 0.528 $^{*}$ | -0.440 $^{**}$ | 0.006 $^{NS}$ | -0.657 $^{*}$ | 0.291 $^{NS}$ | -0.043 $^{NS}$ |
| *Galium triflorum* | 0.0041 | 0.49 | -0.852 $^{**}$ | -0.053 $^{NS}$ | 0.016 $^{NS}$ | -0.569 $^{NS}$ | -0.947 $^{***}$ | 0.237 $^{NS}$ |
| *Lathyrus palustris* | 0.0011 | 0.57 | 0.225 $^{NS}$ | -0.184 $^{NS}$ | -0.331 $^{NS}$ | -0.766 $^{*}$ | 0.103 $^{NS}$ | -0.223 $^{NS}$ |
| *Zizia aurea* | 0.0023 | 0.53 | 0.826 $^{**}$ | -0.325 $^{NS}$ | 0.420 $^{NS}$ | 0.012 $^{NS}$ | 0.580 $^{*}$ | -0.314 $^{NS}$ |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS - not significant $P > 0.05$.

† Disturbance variables include: AP - site area to perimeter ratio; CanCov - canopy cover; Conn - site connectivity which measures the area, perimeter and distance to nearby forest; DF - the proportion of degraded forest (any section of forest with a dimension < 30 m) within a 1000 m radii; Dstrb - site level disturbance from no disturbance (1) to severley disturbed (10); Grbg - cover of garbage presen

‡ Environmental variables include: Clay - soil percent clay; Ec - electrical conductivity; PSM - percent soil moisture; Sand - soil percent sand; Topo - topography from flat (1) to ridge and swale (4).

§ Standardized beta is a standardized partial regression coefficient (Zar 1996).

#Bold faced species indicates exotic origin.

††All *Carex* species grouped together.

garbage ($P < 0.0001$) (Table 5.2a). In contrast, occurrences of native species, such as *G. triflorum* ($r^2 = 0.57$, df = 6,18, $P = 0.0011$) and *R. idaeus* ($r^2 = 0.59$, df = 6,18, $P = 0.0007$), were significantly and negatively associated with disturbance, and both decreased with intensity of disturbance ($P = 0.002$ and $P = 0.001$, respectively) (Table 5.2a).

Environmental variables significantly ($P < 0.005$) predicted the occurrence of seven species, all of which were native. Of these, only *G. triflorum* was significantly predicted by both environment and disturbance. Percent clay and percent sand both had the greatest effect on species occurrence, although all environmental variables, except topography, were significantly associated with at least one species (Table 5.2b). For example, occurrence of native *A. alnifolia* ($r^2 = 0.56$, df = 6,18, $P = 0.0014$) was positively associated with percent clay ($P = 0.0113$), sand ($P = 0.001$), and soil moisture ($P = 0.0083$), and negatively associated with electrical conductivity ($P = 0.0422$). In contrast, occurrence of native *G. triflorum* ($r^2 = 0.49$, df = 6,18, $P = 0.0041$) was negatively associated with percent clay ($P = 0.0069$) and sand ($P = 0.001$).

## VULNERABILITY:OPPORTUNISTIC RANKING

The majority (69 %) of the understorey plant community were generalist species that have relatively little preference for either city or non-city land use types (Appendix 5). In contrast, vulnerable (15 %) and opportunistic (16 %) species were less common in the understorey as a whole, and responded differently to city and non-city land use. All of the 20 most common species were generalists, whereas the highest ranked vulnerable and opportunist species were only ranked 37th and 24th in abundance, respectively (Table 5.3). In general, the most vulnerable species (VI1) were less common than less vulnerable

**Table 5.3.** Characterization of plant species occurring in the riparian forest along the Assiniboine River, classified according to their vulnerable or opportunistic response to disturbance.

| Species and grouping by | | | | Guilds# | | | | Occurrence rank†† | | |
|---|---|---|---|---|---|---|---|---|---|---|
| V:O ratio | V:O† | VI‡ | OI§ | Or | Lf | Ph | Dt | Tot | Cy | NCy |
| VI1 (infinity) | | | | | | | | | | |
| *Scutellaria lateriflora* | $6^{E+11}$ | $6^{E+11}$ | 0.00 | N | PF | S | BAR | 72 | - | 60 |
| *Apocynum cannabinum* | $4^{E+11}$ | $4^{E+11}$ | 0.00 | N | PF | S | ANE | 93 | - | 74 |
| *Carex brunnescens* | $4^{E+11}$ | $4^{E+11}$ | 0.00 | N | PG | S | BAR | 82 | - | 63 |
| *Polygonum coccineum* | $4^{E+11}$ | $4^{E+11}$ | 0.00 | N | PF | F | END | 118 | - | 105 |
| *Salix interior* | $4^{E+11}$ | $4^{E+11}$ | 0.00 | N | W | S | BAR | 124 | - | 111 |
| *Scirpus fluviatilis* | $4^{E+11}$ | $4^{E+11}$ | 0.00 | N | PG | S | EPI | 125 | - | 112 |
| *Ranunculus abortivus* | $2^{E+11}$ | $2^{E+11}$ | 0.00 | N | BF | S | ANE | 81 | - | 62 |
| VI2 (5 < V:O < 15) | | | | | | | | | | |
| *Aster simplex* | 10.00 | 10.00 | 0.10 | N | PF | F | ANE | 47 | 105 | 34 |
| *Stachys tenuifolia* | 9.94 | 10.00 | 0.11 | N | PF | S | BAR | 50 | 111 | 38 |
| *Matteuccia struthiopteris* | 9.86 | 10.00 | 0.12 | N | PF | F | ANE | 37 | 61 | 30 |
| *Rubus idaeus* | 8.13 | 8.00 | 0.11 | N | W | E | END | 41 | 102 | 29 |
| *Carex assiniboinensis* | 7.83 | 8.00 | 0.15 | N | PG | S | BAR | 55 | 83 | 47 |
| *Phryma leptostachya* | 7.83 | 8.00 | 0.15 | N | PF | F | EPI | 38 | 68 | 32 |
| *Phalaris arundinacea* | 7.41 | 8.00 | 0.21 | N | PG | S | ANE | 80 | 117 | 65 |
| *Convolvulus sepium* | 5.89 | 6.00 | 0.19 | E | PF | S | EPI | 86 | 86 | 76 |
| *Carex aquatilis* | 5.60 | 6.00 | 0.25 | N | PG | S | BAR | 87 | 96 | 72 |
| *Carex sprengelii* | 5.60 | 6.00 | 0.25 | N | PG | S | BAR | 67 | 114 | 57 |

**Table 5.3**. Continued

| Species and grouping by V:O ratio | V:O† | VI‡ | OI§ | Guilds# Or | Lf | Ph | Dt | Occurrence rank†† Tot | Cy | NCy |
|---|---|---|---|---|---|---|---|---|---|---|
| *Mentha arvensis* | 5.38 | 6.00 | 0.30 | N | PF | F | BAR | 102 | 110 | 91 |
| *Helianthus tuberosus* | 5.09 | 6.00 | 0.37 | N | PF | F | END | 99 | 116 | 83 |
| OI2 ($0.1 < V:O < 0.5$) | | | | | | | | | | |
| *Plantago major* | 0.50 | 0.00 | 1.00 | E | PF | F | END | 106 | 92 | 104 |
| *Artemisia absinthium* | 0.40 | 0.00 | 1.50 | E | PF | F | ANE | 76 | 57 | 88 |
| *Glechoma hederacea* | 0.40 | 0.00 | 1.50 | E | PF | E | BAR | 89 | 67 | 89 |
| *Urtica dioica* | 0.40 | 0.00 | 1.50 | E | PF | F | END | 104 | 82 | 106 |
| *Chenopodium album* | 0.31 | 0.00 | 2.25 | E | AF | F | END | 110 | 81 | 115 |
| *Rumex crispus* | 0.31 | 0.00 | 2.25 | E | PF | S | ANE | 103 | 76 | 116 |
| *Viola canadensis* | 0.31 | 0.00 | 2.25 | N | PF | E | MYR | 117 | 95 | 114 |
| *Cotoneaster melanocarpa* | 0.25 | 0.00 | 3.00 | E | W | E | END | 122 | 103 | 118 |
| *Elymus canadensis* | 0.25 | 0.00 | 3.00 | N | PG | S | ANE | 123 | 106 | 119 |
| *Sorbus decora* | 0.25 | 0.00 | 3.00 | N | W | S | END | 119 | 108 | 113 |
| *Rhamnus cathartica* | 0.22 | 0.22 | 4.50 | E | W | E | END | 24 | 3 | 85 |
| *Trifolium repens* | 0.21 | 0.00 | 3.75 | E | PF | F | END | 98 | 78 | 101 |
| *Lonicera tartarica* | 0.13 | 0.00 | 6.75 | E | W | S | END | 71 | 46 | 109 |
| OI1 (approaching 0) | | | | | | | | | | |
| *Caragana arborescens* | $5^{E-12}$ | 0.00 | $2^{E+11}$ | E | W | S | AUT | 74 | 44 | - |
| *Comandra umbellata* | $5^{E-12}$ | 0.00 | $2^{E+11}$ | N | PF | E | END | 114 | 79 | - |
| *Hesperis matronalis* | $5^{E-12}$ | 0.00 | $2^{E+11}$ | E | PF | S | AUT | 92 | 56 | - |

**Table 5.3.** Continued

| Species and grouping by | | | | Guilds# | | | | Occurrence rank†† | | |
|---|---|---|---|---|---|---|---|---|---|---|
| V:O ratio | V:O† | VI‡ | OI§ | Or | Lf | Ph | Dt | Tot | Cy | NCy |
| *Campanula rapunculoides* | $3^{E-12}$ | 0.00 | $3^{E+11}$ | E | PF | S | ANE | 109 | 75 | - |
| *Chenopodium hybridum* | $3^{E-12}$ | 0.00 | $3^{E+11}$ | N | AF | F | END | 121 | 91 | - |
| *Setaria viridis* | $3^{E-12}$ | 0.00 | $3^{E+11}$ | E | AG | S | EPI | 120 | 89 | - |
| *Solanum dulcamara* | $2^{E-12}$ | 0.00 | $5^{E+11}$ | E | W | S | END | 53 | 23 | - |

† Ratio of vulnerability over opportunism.

‡ Vulnerability idex, defined as the proportion of reference sites (N = 5) in which a species occurred, divided by the proportion of city sites (N = 10) in which a species occurred.

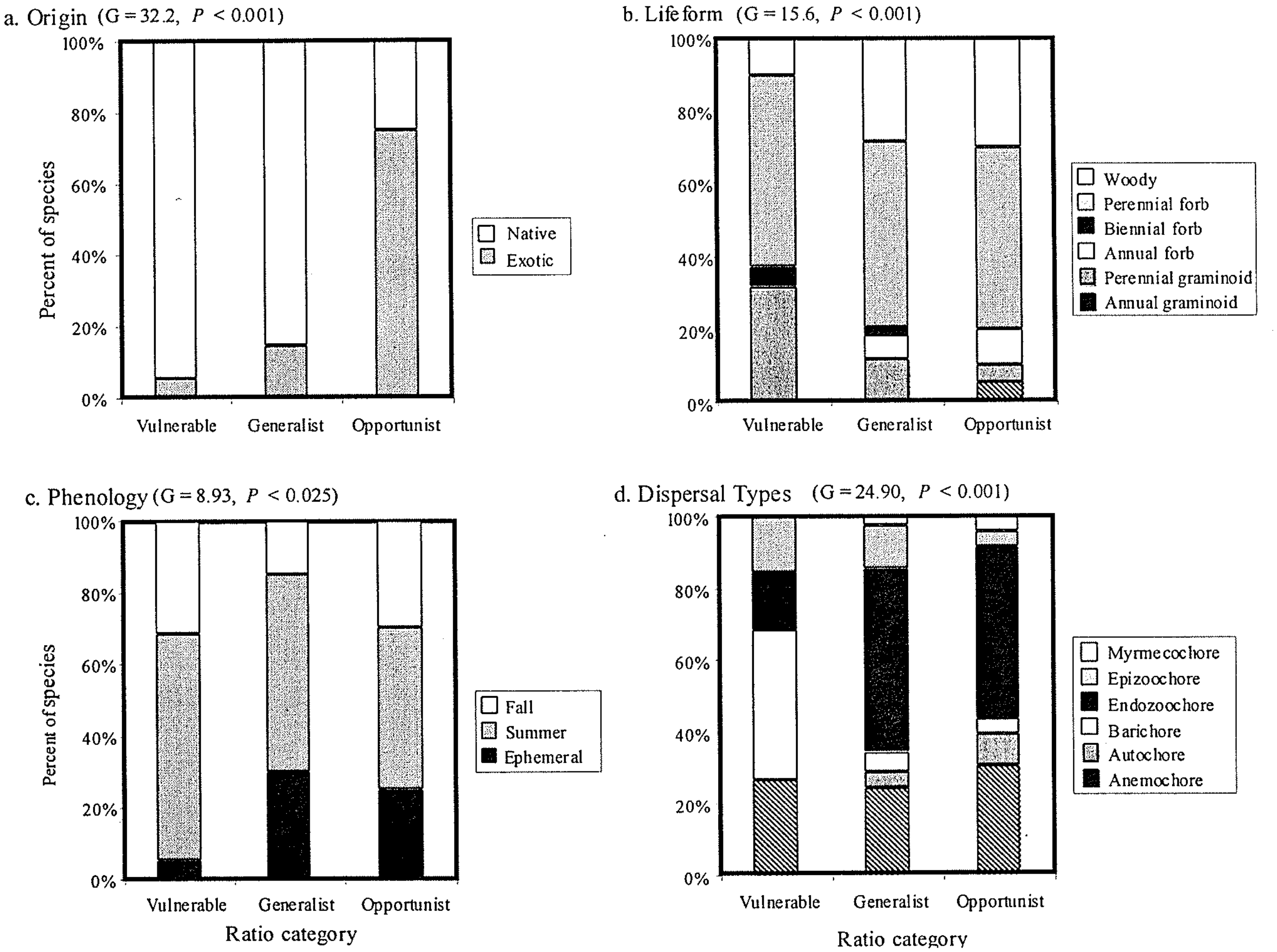
§ Opportunism index defined as the proportion of city sites (N = 10) in which a species occurred, divided by the proportion of non-city sites (N = 15) in which a species occurred.

#Functional Guilds: Or, origin (E - exotic, N - native); Lf, plant lifeform (AG - annual graminoid, PC graminoid, AF - annual forb, BF - biennial forb, PF - perrenial forb, W- woody); Ph, flowering phenology (E - ephemeral herbs flowering March - May, S - summer herbs flowering June - August, F - fall herbs flowering September - November); Dt, dispersal type (ANE - anemochore wind-dispersed, AUT - autochore explosion-dispersed, BAR - barichore gravity-dispersed, END - endozoochore animal-consumed, EPI - epizoochore animal-carried, MYR - myrmecochore ant-dispersed).

††Proportional occurrence of each species ranked in decreasing occurrence from most frequent (1) based on: Tot - all species (N = 126); Cy - species in city sites (N = 117); NCy - species in non-city sites (N = 119).

species (VI2), having mean total rankings of 99th and 66th, respectively. The most vulnerable and less vulnerable species also had mean non-city rankings of 83rd and 54th, respectively (Table 5.3). In contrast, when opportunistic species were examined, there was no difference in occurrence among the most (OI1) and less opportunistic (O12) species, which had mean total rankings of 98th and 97th, respectively (Table 5.3).

The ratio of vulnerability to opportunism, calculated as an overall index of the differential response to land use, was significantly associated with species origin ($P < 0.001$), plant life form ($P < 0.001$), flowering phenology ($P < 0.025$), and seed dispersal ($P < 0.001$) guilds (Fig. 5.2). Eighteen of the 19 vulnerable (VI1 and VI2) species and all of the most vulnerable (VI1) species were native in origin. In contrast, only five of the 20 opportunistic (OI1 and OI2) species were native (Table 5.3, Fig. 5.2). Vulnerable species tended to be perennial grasses and forbs, and never were annual grasses or forbs. In contrast, opportunistic species were more likely to be annual and woody and less likely to be perennial grasses. Vulnerable species were more likely to be summer flowering, and *R. idaeus* was the only vulnerable ephemeral. In contrast, opportunistic species were more likely to be ephemeral. Vulnerable species generally were more likely to have restricted dispersal as barichores, than were opportunistic species, which were more effective dispersers as endozoochores and epizoochore. Myrmecochores were rare overall. Absent from vulnerable species, it only occurred once among opportunist species.


a. Origin (G = 32.2, $P < 0.001$)

b. Lifeform (G = 15.6, $P < 0.001$)

c. Phenology (G = 8.93, $P < 0.025$)

d. Dispersal Types (G = 24.90, $P < 0.001$)

**Fig. 5.2**. Percentage of vulnerable (VI1 and VI2, N = 19), generalist (VI3 – OI3, N = 87), and opportunist (OI2 and OI1, N = 20) species that belong to different functional guilds. Functional guilds include (a) origin, (b) life form, (c) phenology, and (d) dispersal type.

## INDICATORS

In order to identify species that would be strong indicators of forest integrity, I correlated species diversity with those species that had significantly responded to land use, those that had significantly responded to disturbance and environmental variables, or those that had been identified as either vulnerable or opportunistic. Of the 56 species that significantly related to one of these three measures, 48 were significantly correlated ($P < 0.05$) with diversity (Appendix 6).

Three of those indicator species correlated with diversity, *S. dulcamara*, *Carex* spp., and *R. idaeus*, were significantly associated with all three measures and identified as the "best" class of indicators (Table 5.4). For example, the exotic opportunistic species *S. dulcamara* was positively associated with urban land use, disturbance, and the diversity of opportunist species, and in turn, negatively associated with total, native, and vulnerable species diversity. In contrast the native vulnerable taxon, *Carex* spp. showed the opposite response to urban land use, disturbance, and diversity (Table 5.4). Similarly, the native vulnerable species *R. idaeus* was positively associated with rural and non-city land use, negatively associated with disturbance and opportunist species diversity, and positively associated with total, native, and vulnerable species diversity.

Eleven of those 48 indicator species correlated with diversity were associated with two of the three measures and identified only as "good" indicators. For example, *Phalaris arundinacea,* a native vulnerable species was negatively associated with disturbance and positively associated with total, native, and vulnerable species diversity. In turn, *G. triflorum,* a native generalist was positively associated with non-city and specifically rural land use, and with native and vulnerable species diversity, whereas it was negatively

**Table 5.4.** Summary list of most effective indicator species showing their V:O ratio classification and significant relations with measures of land use, disturbance variables, and diversity.

|  | V:O | Land use§ |  |  |  | Disturbance | Hill diversity†† |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Indicator Species† | Ratio‡ | Ur | Ru | Cy | Ncy | Variable# | E | N | T | V | O |
| Best |  |  |  |  |  |  |  |  |  |  |  |
| *Carex* spp. ‡‡ | VI2 | - |  |  |  | - |  | + | + | + |  |
| *Rubus idaeus* | VI2 |  | + |  | + | - |  | + | + | + | - |
| ***Solanum dulcamara*** | OI1 | + |  |  |  | + |  | - | - | - | + |
| Good |  |  |  |  |  |  |  |  |  |  |  |
| *Amelanchier alnifolia* |  | - |  |  |  |  |  | + | + |  |  |
| *Aster simplex* | VI2 |  | + |  | + |  |  | + | + | + | - |
| *Chenopodium hybridum* | OI1 | + |  |  |  |  |  | - | - |  |  |
| *Galium triflorum* |  |  | + |  | + | - |  | + |  | + | - |
| ***Lonicera tartarica*** | OI2 | + |  | + |  |  | + |  |  | - | + |
| *Phalaris arundinacea* | VI2 |  |  |  |  | - |  | + | + | + |  |
| *Ranunculus abortivus* | VI1 |  |  |  |  | - |  |  |  | + |  |
| ***Rhamnus cathartica*** | OI2 | + |  | + |  |  |  |  |  | - | + |
| ***Setaria viridis*** | OI1 | + |  |  |  |  |  | - | - |  |  |
| *Stachys tenuifolia* | VI2 |  | + |  | + |  | - | + | + | + | - |
| ***Urtica dioica*** | OI2 |  |  |  |  | +- |  | - | - |  |  |

† Best and good categories relate to three and two of the measures respectively and correlate with diversity, bold faced species indicate exotic origin.

‡ Vulnerable: opportunistic ratio class, for definition see Table 3 and Appendix 1.

§ Land use classes: Ur, urban; Ru, rural; Cy, city; Ncy, non-city. For proportional occurrence see Table 1.

\# For identification and strength of variables see Table 2

†† Hill diversity includes $N_2$ (dominant species) and $N_0$ (species richness) for: E, exotic; N, native; T, total; V, vulnerable (VI1 + VI2); O, opportunist (OI1 + OI2).

‡‡ Includes all *Carex* species grouped together.

associated with disturbance and opportunist species diversity. Finally, the native *C. hybridum* and exotic *S. viridis* opportunistic species were only found in urban sites, and were both negatively associated with total and native species diversity. Importantly, the 14 effective indicator species reflected all four of the previously identified general responses to land use (i.e. urban exploiters, urban avoiders, city, and non-city) and are, thus, appropriate for use along the entire urban-rural gradient.

## 5.4 Discussion

My results show that understorey herbaceous species, both individually and grouped according to functional types or guilds, are effective indicators of environmental change and disturbance associated with land use. I identified two categories of specie response to urban land use: "opportunistic species", which were either restricted to or dominated disturbed forests, and " vulnerable species", which were excluded from disturbed forests. "Urban exploiters" and "urban avoiders" were similarly found for avifauna in California (Blair 1996), in part, because exotic and native birds tend to frequent exotic and native plant species, respectively (Mills et al. 1989). A subset of plant species was associated with both urban and suburban sites (i.e. city sites), in contrast to those that were found more frequently in rural and reference sites (i.e. non-city sites). This suggests that suburban sites are intermediate in disturbance (McDonnell et al. 1993) and compositionally distinct from rural sites (Chapter 3).

Origin was an important predictor of response to land use. Species associated with urban or city land use were generally exotic and effective indicators of disturbance, reflecting that extant urban forest in Southern Manitoba is severely disturbed, isolated, small in size, and characterized by dry, alkaline soils, and extensive amounts of garbage (Chapter 3). For example, *Solanum dulcamara* was exclusively found in urban sites and strongly associated with the presence of garbage. *Rhamnus cathartica*, a city species, was primarily associated with suburban land use, is highly invasive of disturbed forests in North America (Archibold et al. 1997), and appears to out-compete native tree species in urban forests of southern Manitoba (Winnipeg Natural Services Branch 2001) and Boston (Drayton & Primack 1996). All indicators of disturbance were opportunistic, and the majority of these (85 %) as well as opportunistic species as a whole (75 %) were exotic. Generally exotic plant species tend to flourish in disturbed environments often replacing native species (Rudnicky & McDonnell 1989).

Life form also helped determine understorey response to land use. Although perennial forb was the most common life form in this study, indicator species of disturbance were characterized by woody or annual life form. Woody species tend to be more resistant to disturbance, perhaps because of their relatively longer life spans and greater structural durability (Robinson et al. 1994). Disturbed secondary forests in eastern U.S.A. had more woody brush than relatively undisturbed primary forests (Duffy & Meier 1992). Similarly, invasive indicators of disturbance are often woody (e.g., *Lonicera tartarica* (Woods 1993), *R. cathartica* (Drayton & Primack 1996) and *Acer platanoides* (Webb & Kalafus-Kaunzinger 1993) and are often escaped horticultural species (Archibold et al. 1997). In turn, annuals tend to respond positively to disturbance, in part because of their rapid rates of biomass production and abundant seed production (Bazzaz 1979). The latter was reflected in the seed bank of my disturbed sites (Chapter 4).

Indicator species of disturbance in this study tended to be endozoochores that produce berries. In highly fragmented landscapes dominated by a hostile matrix such as urban cover, animal dispersers generally deliberately visit remnant habitat and exhibit increases in home range size (e.g., Redpath 1995), thus likely increasing the relative effectiveness of animal dispersed seed dispersal under these conditions. Although wind-dispersed seeds, typically have greater dispersal distances (Wilson 1992), their dispersal patterns are largely random and non-selective (Van der Pijl 1972) and therefore likely to exhibit higher mortality rates in highly fragmented urban environments. Dispersal-restricted species, those that are gravity-, explosion-, or ant-dispersed, often travel only centimeters per year and are generally unable to traverse the gaps that separate urban patches (Dzwonko & Loster 1992).

Species associated with non-city land use and, more specifically, with low-intensity rural land use were, as anticipated, effective indicators of high integrity forests, reflecting that rural forests tended to be least disturbed, larger in size, and better connected than their urban and suburban counterparts (Chapter 3). For example, both *Rubus idaeus* and *Gallium triflorum* were effectively absent from urban and suburban sites, positively associated with low-intensity rural land use and negatively associated with disturbance. Nearly all (95 %) vulnerable species were native, as were all species identified as effective indicators of high integrity forests. Thus, native species seemed to be disproportionately affected by forest fragmentation, and many were excluded from the highly disturbed urban sites (e.g., Robinson et al. 1994; Drayton & Primack 1996).

Generally vulnerable species and indicators of high integrity forests were perennial. If herbaceous, perennials tend to be relatively susceptible to disturbance as they often produce fewer seeds and have non-persistent seedbanks (Primack & Miao 1992). As with other studies on forests in eastern North America (e.g., Matlack 1994b), indicator species of my high integrity forests were often dispersal-restricted barichores, suggesting that these dispersal strategies tend to be less effective for environments dominated by hostile urban matrices.

Other studies of degraded forests have found that myrmecochores (Dzwonko & Loster 1992) and ephemerals (McLachlan & Bazely 2001) are vulnerable to fragmentation and disturbance. In addition to being barichores, vulnerable species in my study also tended to be summer flowering. Indeed, none of the identified vulnerable species were myrmecochores. The ephemerals present in these forests were generally early successional (e.g., *R. idaeus*) or invasive (e.g., *R. cathartica*), instead of late successional species that might otherwise characterize the understorey, thus suggesting that the extant forest throughout this system might be degraded. Populations of late successional ephemeral and ant dispersed species might have previously been reduced (e.g., *Viola pubescens*) or eliminated from the understorey by large-scale disturbance. Moreover, had these species exhibited declines across all the land use types, they would not have been identified as indicators in my study, which required a differential response among land use types. Ephemerals might otherwise have represented a larger proportion of the vulnerable species, however much of the remaining rural forest has been extensively used for lumber and firewood. More recently, the overstorey in these sites has been further opened with elm mortality, thus creating gaps that may negate the relatively competition-free temporal niche normally occupied by spring-flowering plants (Meier et al. 1995). Finally, studies documenting the dominance of myrmecochores in hardwood forests as well as their relative vulnerability to disturbance have been conducted in southern Canada (McLachlan & Bazely 2001) and eastern U.S.A. (Beattie & Culver 1981). Dispersal restricted species in my study may be at the northern limits of their distribution ranges, and, historically, may never have been an important component of the understorey in these forest systems.

As many of the indicators of disturbance are Eurasian in origin, they are likely common in many urban forest remnants across North America, and indeed some (e.g., *R. cathartica* (Drayton & Primack 1996; Archibold et al.1997) and *L. tartarica* (Woods

1993) have been identified as problematic invasive species. As urban expansion continues, the need to understand the mechanisms that underlie invasion by exotics and their use as indicators for management of degraded extant forest is increasing in relevance (McDonnell & Pickett 1990). However, most small urban forests remain relatively understudied and, indeed, undervalued (Shafer 1995).

Presently, extant riparian urban forest in Winnipeg is ranked into four non-quantitative classes of quality according to relative presence of herbaceous, weedy, exotic, and woody vegetation, and the human alteration of vegetation cover and stream-bank (Shaluk unpubl.). None of the extant forest in this area has been ranked as 'A' (pristine), and only that which has been ranked as 'B' (slightly disturbed by human trails) or higher is then fully characterized. This ranking is quick, reflects similar provincial ranking approaches (C. Hemming pers. comm.), and, in the absence of ground-level data, is adequate for managers and policy makers.

This use of indicator species or guilds would allow managers to more accurately assess the quality of these forests without requiring an exhaustive description of the understorey. In my study, when exotic and native diversity were analyzed separately, indicator species functioned as effective indicators of habitat quality and diversity. Indicator species of disturbance typically were associated with low native diversity whereas indicator species of high integrity forests were typically associated with high native diversity. Although commonly prescribed, the use of species or taxa as indicators of changes in biodiversity recently has been criticized (e.g., Prendergast & Eversham 1997; Lawton et al. 1998). Guilds have great promise as management tools as they are more generalizable than site-specific changes in plant population, or species composition, on one hand or changes in diversity, which are often too coarse to be very useful, on the other (Hobbs 1997). The life form, seed dispersal and flowering guilds used in this study were effective predictors of opportunism and vulnerability associated with land use; opportunistic species tended to be exotic, woody, and endozoochores, whereas vulnerable species tended to be native, perennial, and barichores or anemochores.

Most of the riparian forest patches in this human-dominated landscape are privately owned. Although there is strong interest by landowners in the quality of their riparian forest (Moffatt pers. obs.) they may not have the resources to fully characterize the understorey. These indicator species and guilds hold much promise and are accessible for use by concerned residents and community groups that frequent these forests. The response of stakeholders to these types of expert-based indicators of habitat quality is of great importance (Schiller et al. 2001) and will be investigated more fully in the future.

As urban and suburban development continues, extant forest is increasingly threatened. Indeed, in the course of this study, two of my five suburban forest sites were cleared for housing, as were other surrounding forest patches (Moffatt pers. obs.). This pattern of increased residential development and its effects on remnant forests is common across North America (Matlack 1997b). As the seed bank exhibited a similar response to disturbance along this urban-rural gradient (Chapter 4) and is also dominated by exotic species, the decline of these forests will likely continue unabated should land use remain unchanged and should future forest regeneration be dependent upon the seed bank. Their protection and active management, whether in the form of native planting or the control of exotics, needs to be considered should this ongoing decline be mitigated.

# CHAPTER 6: Discussion

## SUMMARY

Riparian forests represent an important ecotone between aquatic and terrestrial ecosystems, and play a critical role in the structure and function of rivers. Despite the many ecological and anthropocentric benefits that riparian forests provide, they are increasingly becoming endangered across North America. The extensive landscape modification associated with agriculture and urbanization has resulted in a complex urban to rural land use gradient. Changes in land use are severely fragmenting these riparian forests, leading to habitat loss and increased isolation of remnant patches.

The effects of urban land use were the most severe. Extant urban forest was extremely small (< 0.5 ha), effectively having no interior habitat, and very isolated. Land use has greatly affected both the abiotic and biotic conditions of urban forests. They had dry alkaline soils, were littered with a large amount of garbage, and were highly accessible to human use. Changes in biotic conditions were reflected in both the above and below ground species composition and diversity. The above ground composition of urban forests was dominated by only a few species that were typically exotic and that thrived in the disturbed conditions. One such exotic is *Solanum dulcamara*, which I identified as a strong indicator species of disturbance. As such, it was strongly associated with urban sites, many of the disturbance variables, low overall plant diversity, and was characterized as an opportunistic species. The seed bank composition of urban forests was also characterized by fewer species and was relatively dominated by exotics. The overall and native diversity of both the above ground and the seed bank was lowest in the urban forests compared to the other land uses, whereas the exotic diversity was the highest. Many of the native species seemed to be out-competed by and ultimately replaced by exotic species, that either had originated from the surrounding matrix or were better adapted to growing in disturbed conditions.

Riparian forests surrounded by suburban land use were not as severely disturbed as urban forests; however, they are showing the greatest current change. During the length of this study, several of my suburban forest sites were further cleared for development. Extant suburban forest was larger than urban forest (5.0 ha mean size), although smaller than rural forests. Compositionally, suburban forest flora and seed bank, were not as distinct from rural sites as those of urban forests. However, several of the indicator species of disturbance (e.g., *Rhamnus cathartica* and *Lonicera tartarica*) were strongly associated with suburban land use. Additionally, suburban forests had a higher proportion of exotic species in the above ground and seed bank composition than did those of rural forests. It seems that suburban forests currently represent an intermediate level of disturbance between rural and urban forest. However, as development pressures continue disturbance will increase and the suburban forests will likely increase in similarity to the severely disturbed urban forests.

There was very little difference among high- and low-intensity rural and reference sites. Reference sites were significantly larger than rural sites (47 and 15 ha mean size, respectively), and were better connected. The above ground and seed bank composition of these rural sites had the highest overall diversity and the lowest number of invasive exotic species. All of the species that were indicators of relatively high quality forests were associated with rural land use or excluded from urban forests and they were typically native and vulnerable. For example, *Carex* spp. was excluded from urban forests, whereas *Rubus idaeus* was associated with low-intensity rural. Both species were classified as vulnerable species.

Although generalists dominated (69 %) the forest understorey, only opportunistic and vulnerable species functioned as effective indicators of disturbance and high quality forest respectively. Opportunistic species, defined as those more likely to occur in disturbed city sites, tended to be exotic, woody or annual, and effective dispersers (i.e. endozoochores). In contrast, vulnerable species, defined as those more likely to occur in relatively high quality reference sites, tended to be native, perennial, and ineffective dispersers (i.e. barichores or anemochores).

## FUTURE DIRECTIONS

At the outset of this study, it was intended to look at not only the urban – rural landscape level gradient but also the interaction of this gradient with an edge – interior site level gradient. In order to effectively describe the urban – rural gradient, I was not able to adequately sample edge – interior gradient. Furthermore, the urban sites along the land use gradient lacked any true interior, making it hard to compare the edge – interior response among land use categories. I had anticipated that disturbance from surrounding land use would extend further into the greater disturbed city sites, and although not statistically significant this appeared visually true. A study that effectively demonstrated these differences would have had to have more edge-to-interior sampling and fewer land use categories.

Another direction this study could take is a greater emphasis at the landscape level of organization. Additional layers of data can be digitized and entered into GIS, such as length of roads per unit area, population density, and proximity to and length of paths within study sites. Historical information (aerial photos) of land use could also have been used to quantify changes in forest fragmentation over time in relation to land use. Statistical software such as FragStats or computer modeling could have been used to further quantify landscape level responses to land use disturbance.

Other site level variables could have received further attention. Soil nutrients and organic matter may show a response to land use gradient in relation to application levels of agricultural pesticides and fertilizers. Soil compaction could be and is often used as an indicator of disturbance, which tends to be associated with urban and recreational use. Edge-associated variables that could be measured include wind speed, insolation, and air and soil temperature. Finally elevation, which plays a key role in determining species composition of riparian habitat in relation to water availability and flooding, might have been better measured.

As my study examines changes in species composition and diversity in relation to land use it is largely correlative. The next stage of this project would be to understand the mechanisms that underlie these observations. This might be addressed by examining the differences in competitive ability among native and exotic species, the colonization rates and dispersal differences among species, and species-specific responses to stress. Bill Thompson is conducting a Masters of Science using results from my study and the established study sites. He is examining the role that fragmentation plays in interrupting the dispersal vectors by using seed traps and genetic similarity among model species. Additionally, he is looking at the synergistic effect of fragmentation and urbanization on the myrmecochore guild by categorizing the ant communities in urban and non-urban forests and observing their dispersal of seeds.

Another important aspect and area of growing interest is human perception and use of indicators. This study has developed a list of indicator species that can be used as a management tool for landowners. To do so, however, these indicators need to be both identifiable and understandable to the public as a whole. A study could be developed to work directly with the landowners to test how identifiable and useful these indicators are and work to improve any weaknesses in the indicators.

## MANAGEMENT RECOMMENDATIONS

Extant urban forest is severely disturbed, having very low species diversity and mostly consisting of exotic species. To return these forests to a more natural composition would require a substantial restoration effort. As the seed bank largely consists of annual and ruderal species managers would have to reintroduce many of the lost native species and attempt to remove the exotic seed bank. In order for many of the natives to establish, the stressed conditions associated with these sites would need to be changed, including a reduction in soil compaction and edge habitat. The size of these patches would need to be substantially increased in order to reflect recommended minimum patch size that retains interior habitat. Planting or regeneration would need to increase the patch width to a minimum of 40 m if it is going to support interior habitat. Furthermore, the connectivity among the urban patches and to other forest patches would need to be increased to maintain natural species populations. However, considering the severity of the disturbance and the likely impossible task of increasing patch size I feel that a restoration effort would not be successful. Therefore, I suggest that urban conservation efforts focus on preventing any further fragmentation and retain vegetation to prevent associated bank erosion. Instead of wasting resources on trying to restore the urban forest, I recommend that active management focus on the suburban forests.

The suburban forests, although smaller than rural forests, were still large enough to retain a similar species composition and diversity to high integrity sites, although they have a higher proportion of exotic species. Suburban forests appear to be in a state of transition, and represent a condition between that of rural and that of urban forests. If the increasing fragmentation and disturbance from suburban development continues they will likely continue to deteriorate, and increasingly resemble urban forests. These forests should be protected from any further fragmentation and efforts made to reduce human disturbance, while restoring suburban patches that show more severe disturbance. Restoration would include both the removal of the most competitive exotic species and the reintroduction of lost native species not present in the seed bank. Additionally, an education program for interested community groups could be introduced, where the use of effective indicator species could be promoted. This would allow local community and stewardship groups to monitor the long-term condition of their forests and give them an increased involvement in protection and restoration efforts.

Rural forests show little disturbance relative to the reference forests. Their flora and seed bank compositions, and diversity were very similar, although rural sites were slightly smaller and less connected. These forests can best be managed and protected through education. Many of the landowners were very interested in preserving their forests as they realized the benefit of retaining a riparian buffer. Additionally, by promoting the use of indicator species, they can monitor the condition of their forests without relying on expert help. Where the rural forests have been cleared efforts should be made to restore them, to increase connectivity for the natural dispersal of species, and to stabilize the river banks.

These recommendations are based on a detailed study of the 25 riparian forest study sites. However, I feel that the information generated can be applicable to other areas in particular those along the Assiniboine River. The method the city of Winnipeg currently uses to assess the quality of riparian forest sites is highly subjective. I feel that the application of the 14 identified indicator species, and their associated functional guilds, in conjunction with disturbance variables such as patch size and quantity of garbage could be a quick, easy, and more effective means of assessing forest quality. This method would be applicable to other riparian systems such as the Seine and Red Rivers, although this should be verified.

This study represents the first of its kind as it examines riparian forests in a prairie landscape at different scales of organization. It clearly identifies impacts of surrounding land use on the both the flora and the seed bank. Indicators of disturbance that were identified should be of great use to landowners and managers in the region. Although urban riparian forests are an important factor in Winnipeg, they, along with their suburban counterparts, are clearly degraded and being lost. The decline of these forests will likely continue unabated should land use remain unchanged and should future forest regeneration be dependent upon the seed bank. Their protection and active management, whether in the form of native planting or the control of exotics, needs to be considered should this ongoing decline be mitigated.

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## Appendix 1: Site Description

**Appendix 1**. Location and characterization of sites with coordinates of site center and the proportion of surrounding land use within a 1000 m radii circle.

| | Site Location | | Percent Land Use | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Site | Latitude N | Longitude W | Urban | Suburban | High rural | Low rural | Healthy forest | Degraded forest | River |
| U1 | 49°53.1' | 97°07.8' | 78.0 | 5.2 | 0.0 | 0.0 | 0.9 | 3.1 | 12.8 |
| U2 | 49°53.0' | 97°08.2' | 77.9 | 6.1 | 0.0 | 0.0 | 0.9 | 3.5 | 11.6 |
| U3 | 49°53.0' | 97°08.4' | 80.7 | 4.8 | 0.0 | 0.0 | 0.8 | 3.4 | 10.3 |
| U4 | 49°52.9' | 97°08.6' | 81.3 | 4.5 | 0.0 | 0.0 | 0.6 | 3.6 | 10.0 |
| U5 | 49°52.4' | 97°09.5' | 82.7 | 10.2 | 0.0 | 0.0 | 0.3 | 2.0 | 4.8 |
| S1 | 49°52.4' | 97°12.9' | 0.0 | 89.2 | 0.0 | 0.0 | 3.5 | 2.1 | 5.2 |
| S2 | 49°52.2' | 97°15.9' | 0.0 | 84.1 | 0.0 | 0.0 | 7.9 | 2.6 | 5.4 |
| S3 | 49°52.1' | 97°16.7' | 0.0 | 74.5 | 0.0 | 0.0 | 12.6 | 6.2 | 6.7 |
| S4 | 49°51.8' | 97°17.9' | 0.0 | 85.7 | 0.0 | 0.0 | 6.6 | 2.2 | 5.5 |
| S5 | 49°52.1' | 97°19.4' | 0.0 | 37.8 | 9.6 | 28.3 | 13.1 | 4.0 | 7.2 |
| H1 | 49°51.9' | 97°23.5' | 0.0 | 0.7 | 43.9 | 18.5 | 22.5 | 4.8 | 9.6 |
| H2 | 49°57.2' | 97°37.4' | 0.0 | 21.3 | 53.6 | 1.9 | 13.2 | 4.5 | 5.5 |
| H3 | 49°59.5' | 97°41.4' | 0.0 | 0.0 | 56.0 | 19.7 | 18.4 | 1.2 | 4.7 |
| H4 | 50°00.9' | 97°45.3' | 0.0 | 0.0 | 61.8 | 12.9 | 18.0 | 1.2 | 6.1 |
| H5 | 50°02.5' | 97°49.9' | 0.0 | 0.0 | 71.1 | 3.5 | 17.2 | 0.8 | 7.4 |
| L1 | 49°52.1' | 97°20.7' | 0.0 | 4.6 | 68.7 | 11.4 | 6.1 | 2.8 | 6.4 |
| L2 | 49°52.1' | 97°25.6' | 0.0 | 0.0 | 58.9 | 12.8 | 18.4 | 2.5 | 7.4 |
| L3 | 49°52.4' | 97°28.5' | 0.0 | 0.0 | 71.2 | 12.2 | 10.0 | 1.8 | 4.8 |
| L4 | 49°55.8' | 97°35.2' | 0.0 | 0.0 | 67.5 | 10.1 | 15.4 | 0.4 | 6.6 |
| L5 | 50°00.0' | 97°43.4' | 0.0 | 0.0 | 45.3 | 16.4 | 29.7 | 1.3 | 7.3 |
| R1 | 49°51.8' | 97°17.4' | 0.0 | 76.4 | 0.0 | 0.0 | 11.3 | 4.0 | 8.3 |
| R2 | 49°51.6' | 97°28.2' | 0.0 | 0.0 | 17.6 | 28.7 | 43.6 | 0.6 | 9.5 |
| R3 | 49°51.8' | 97°28.1' | 0.0 | 0.0 | 12.8 | 26.7 | 48.6 | 0.8 | 11.1 |
| R4 | 49°51.9' | 97°29.3' | 0.0 | 2.0 | 14.0 | 35.8 | 40.1 | 0.0 | 8.1 |
| R5 | 50°00.4' | 97°48.5' | 0.0 | 0.0 | 59.5 | 6.3 | 25.1 | 1.2 | 7.9 |

## Appendix 2: Species List

**Appendix 2**. Species found in the above ground flora and seed bank, ranked separately according to frequency of occurrence. Species code used in analysis is given.

| Scientific Name | Common Name | Code | Rank |
|---|---|---|---|
| **Tree species** | | | |
| *Acer negundo* | Manitoba Maple | AceNeg | 2 |
| *Fraxinus nigra* | Black Ash | FraNig | 93 |
| *Fraxinus pennsylvanica* | Green Ash | FraPen | 1 |
| *Populus tremuloides* | Aspen Poplar | PopTre | 64 |
| *Quercus macrocarpa* | Bur Oak | QueMac | 19 |
| *Salix amygdaloides* | Peach-leaved Willow | SalAmy | 132 |
| *Salix discolor* | Pussy Willow | SalDis | 154 |
| *Tilia americana* | Basswood | TilAme | 14 |
| *Ulmus americana* | American Elm | UlmAme | 17 |
| *Viburnum lentago* | Nannyberry | VibLen | 60 |
| **Shrub species** | | | |
| *Amelanchier alnifolia* | Saskatoon | AmeAln | 23 |
| *Caragana arborescens* | Common Caragana | CarArb | 73 |
| *Celastrus scandens* | Climbing Bittersweet | CelSca | 89 |
| *Cornus stolonifera* | Red-Osier Dogwood | CorSto | 20 |
| *Corylus cornuta* | Beaked Hazlenut | CorCor | 40 |
| *Cotoneaster melanocarpa* | Cotoneaster | CotMel | 137 |
| *Crataegus crysocarpa* | Hawthorn | CraCry | 48 |
| *Lonicera dioica* | Twining Honeysuckle | LonDio | 56 |
| *Lonicera tartarica* | Tartarian Honeysuckle | LonTar | 76 |
| *Menispermum canadense* | Yellow Parilla | MenCan | 34 |
| *Parthenocissus quinquefolia* | Virginia Creeper | ParQui | 12 |
| *Prunus americana* | American Plum | PruAme | 86 |
| *Prunus nigra* | Canada Plum | PruNig | 117 |
| *Prunus virginiana* | Choke Cherry | PruVir | 18 |
| *Rhamnus cathartica* | Buckthorn | RhaCat | 24 |
| *Rhus radicans* | Poison-Ivy | RhuRad | 5 |
| *Ribes americanum* | Wild Black Currant | RibAme | 30 |
| *Ribes oxyacanthoides* | Norhtern Gooseberry | RibOxy | 148 |
| *Rosa acicularis* | Prickly Rose | RosAci | 25 |
| *Rubus idaeus* | Wild Red Raspberry | RubIda | 41 |
| *Salix interior* | Sandbar Willow | SalInt | 136 |
| *Solanum dulcamara* | Bittersweet | SolDul | 63 |

| Scientific Name | Common Name | Code | Rank |
|---|---|---|---|
| *Sorbus decora* | Showy Mountain Ash | SorDec | 126 |
| *Spiraea alba* | Narrow-Leaved Meadowsweet | SpiAlb | 96 |
| *Symphoricarpos albus* | Snowberry | SymAlb | 140 |
| *Symphoricarpos occidentalis* | Western Snowberry | SymOcc | 7 |
| *Viburnum opulus* | High Bush-Cranberry | VibOpu | 65 |
| *Viburnum rafinesquianum* | Downy Arrowwood | VibRaf | 29 |
| *Vitis riparia* | Riverbank Grape | VitRip | 31 |
| **Herbaceous species** | | | |
| *Actaea rubra* | Red Baneberry | ActRub | 50 |
| *Agropyron trachycaulum* | Slender Wheatgrass | AgrTra | 37 |
| *Ambrosia artemesifolia* | Common Ragweed | AmbArt | 164 |
| *Amaranthus retroflexus* | Red-Root Pigweed | AmeRet | 146 |
| *Amphicarpa bracteata* | Hog-Peanut | AmpBra | 15 |
| *Anemone canadensis* | Canada Anemone | AneCan | 28 |
| *Anemone cylindrica* | Long-Fruited Anemone | AneCyl | 158 |
| *Anemone virginiana* | Tall Anemone | AneVir | 129 |
| *Apocynum androsaemifolium* | Spreading Dogbane | ApoAnd | 42 |
| *Apocynum cannabinum* | Indian-Hemp | ApoCan | 91 |
| *Aralia nudicaulis* | Wild Sarsaparilla | AraNud | 16 |
| *Arctium minor* | Lesser Burdock | ArcMin | 27 |
| *Arenaria lateriflora* | Blunt-Leaved Sandwort | AreLat | 62 |
| *Artemisia absinthium* | Absinthe | ArtAbs | 84 |
| *Artemisia ludovicia* | Prairie Sage | ArtLud | 157 |
| *Asclepias ovalifolia* | Dwarf Milkweed | AscOva | 105 |
| *Asparagus officinalis* | Asparagus | AspOff | 103 |
| *Aster ciliolatus* | Lindley's Aster | AstCil | 68 |
| *Aster laevis* | Smooth Aster | AstLae | 145 |
| *Aster simplex* | Small Blue Aster | AstSim | 45 |
| *Bidens frondosa* | Common Beggarticks | BidFro | 97 |
| *Botrychium virginianum* | Virginia Grap Fern | BotVir | 106 |
| *Bromus ciliatus* | Fringed Brome | BroCil | 152 |
| *Bromus inermis* | Smooth Brome | BroIne | 10 |
| *Campanula rapunculoides* | Creeping Bluebell | CamRap | 110 |
| *Cardamine pensylvanica* | Bitter Cress | CardPe | 161 |
| *Carex alopecoidea* | Foxtail Sedge | CarAlo | 130 |
| *Carex aquatilis* | Water Sedge | CarAqu | 85 |
| *Carex assiniboinensis* | Assiniboine Sedge | CarAss | 54 |
| *Carex brunnescens* | Brownish Sedge | CarBru | 80 |

| Scientific Name | Common Name | Code | Rank |
|---|---|---|---|
| *Carex convoluta* | Sedge | CarCon | 122 |
| *Carex cristatella* | Prickly Sedge | CarCri | 107 |
| *Carex deweyana* | Dewey's Sedge | CarDew | 44 |
| *Carex laeviconica* | Smooth-Fruited Sedge | CarLae | 123 |
| *Carex peckii* | Peck's Sedge | CarPec | 26 |
| *Carex pensylvanica* | Pensylvania Sedge | CarPen | 75 |
| *Carex praegracilis* | Freeway Sedge | CarPra | 108 |
| *Carex sprengelii* | Sprengel's Sedge | CarSpr | 67 |
| *Carex tenera* | Sedge | CarTen | 147 |
| *Chenopodium album* | Lamb's-Quarters | CheAlb | 124 |
| *Chenopodium hybridum* | Maple-Leaved Goosefoot | CheHyb | 138 |
| *Circaea quadrisulcata* | Large Enchanter's-Nightshade | CirQua | 141 |
| *Cirsium arvense* | Canada Thistle | CirArv | 21 |
| *Comandra umbellata* | Bastard Toadflax | ComUmb | 119 |
| *Convallaria majalis* | Lily-of-the-Valley | ConMaj | 163 |
| *Convolvulus sepium* | Hedge Bindweed | ConSep | 87 |
| *Cryptotaenia canadensis* | Honewort | CryCan | 173 |
| *Dactylis glomerata* | Orchard grass | DacGlo | 160 |
| *Echinocystis lobata* | Wild Cucumber | EchLob | 165 |
| *Elymus canadensis* | Canada Wild Rye | ElyCan | 134 |
| *Elymus virginicus* | Virginia Wild Rye | ElyVir | 55 |
| *Epilobium glandulosum* | Northern Willowherb | EpiGla | 162 |
| *Equisetum arvense* | Common Horsetail | EquArv | 33 |
| *Equisetum hymale* | Common Scouring-Rush | EquHym | 66 |
| *Erigeron philadelphicus* | Philadelphia Fleabane | EriPhi | 159 |
| *Erysimum cheiranthoides* | Wormseed Mustard | EryChe | 151 |
| *Fragaria virginiana* | Smooth Wild Strawberry | FraVir | 71 |
| *Galeopsis tetrahit* | Hemp Nettle | GalTet | 116 |
| *Galium boreale* | Northern Bedstraw | GalBor | 35 |
| *Galium triflorum* | Sweet-Scented Bedstraw | GalTri | 13 |
| *Geum aleppicum* | Yellow Avens | GeuAle | 98 |
| *Glechoma hederacea* | Ground-Ivy | GleHed | 92 |
| *Glycyrrhiza lepidota* | Wild Licorice | GlyLep | 82 |
| *Hackelia virginiana* | Virginia Stickseed | HacVir | 72 |
| *Helianthus tuberosus* | Jerusalem Artichoke | HelTub | 99 |
| *Heracleum lanatum* | Cow-Parsnip | HerLan | 88 |
| *Hesperis matronalis* | Dame's-Rocket | HesMat | 100 |
| *Hieracium umbellatum* | Canada Hawkweed | HieUmb | 133 |

| Scientific Name | Common Name | Code | Rank |
|---|---|---|---|
| *Lactuca scariola* | Prickly Lettuce | LacSca | 142 |
| *Laportea canadensis* | Wood Nettle | LapCan | 47 |
| *Lathyrus ochroleucus* | Cream-Colored Vetchling | LatOch | 51 |
| *Lathyrus palustris* | Marsh Vetchling | LatPal | 102 |
| *Lathyrus venosus* | Wild Peavine | LatVen | 94 |
| *Leonurus cardiaca* | Motherwort | LeoCar | 113 |
| *Lycopus americana* | Water-Horehound | LycAme | 121 |
| *Lycopus uniflorus* | Northern Water-Horehound | LycUni | 135 |
| *Lysimachia ciliata* | Fringed Loosestrife | LysCil | 83 |
| *Lythrum salicaria* | Purple Loosestrife | LytSal | 172 |
| *Maianthemum canadense* | Two-Leaved Solomon's-Seal | MaiCan | 9 |
| *Matteuccia struthiopteris* | Ostrich Fern | MatStr | 36 |
| *Medicago lupulina* | Black Medick | MedLup | 81 |
| *Medicago sativa* | Alfalfa | MedSat | 150 |
| *Melilotus alba* | White Sweet-Clover | MelAlb | 59 |
| *Melilotus officinalis* | Yellow Sweet-Clover | MelOff | 118 |
| *Mentha arvensis* | Field Mint | MenArv | 104 |
| *Mirabilis nyctaginea* | Heart-Leaved Umbrellawort | MirNyc | 131 |
| *Muhlenbergia glomerata* | Bog Muhly | MuhGlo | 153 |
| *Muhlenbergia racemosa* | Marsh Muhly | MuhRac | 170 |
| *Oenothera biennis* | Yellow Evening-Primrose | OenBie | 156 |
| *Oryzopsis asperifolia* | White-Grained Rice Grass | OryAsp | 69 |
| *Osmorhiza longistylis* | Blunt-Fruited Sweet Cicely | OsmLon | 46 |
| *Oxalis europaea* | Yellow Wood-Sorrel | OxaEur | 53 |
| *Parietaria pensylvanica* | American Pellitory | ParPen | 128 |
| *Phalaris arundinacea* | Reed Canary Grass | PhaAru | 78 |
| *Phryma leptostachya* | Lopseed | PhrLep | 38 |
| *Plantago major* | Common Plantain | PlaMaj | 109 |
| *Plantago media* | Hoary Plantain | PlaMed | 52 |
| *Poa palustris* | Fowl Blue Grass | PoaPal | 95 |
| *Poa pratense* | Kentucky Blue Grass | PoaPra | 6 |
| *Polygonatum biflorum* | Solomon's Seal | PolBif | 79 |
| *Polygonatum canaliculatum* | Great Solomon's Seal | PolCan | 114 |
| *Polygonum coccineum* | Swamp Persicaria | PolCoc | 127 |
| *Polygonum convolvulus* | Wild Buckwheat | PolCon | 139 |
| *Potentilla anserenia* | Silverweed | PotAns | 167 |
| *Potentilla norvegica* | Rough Cinquefoil | PotNor | 149 |
| *Ranunculus abortivus* | Smooth-Leaved Buttercup | RanAbo | 77 |

| Scientific Name | Common Name | Code | Rank |
|---|---|---|---|
| *Rubus pubescens* | Dewberry | RubPub | 74 |
| *Rumex crispus* | Curled Dock | RumCri | 111 |
| *Rumex maritimus* | Golden Dock | RumMar | 125 |
| *Sanicula marilandica* | Snakeroot | SanMar | 57 |
| *Scirpus fluviatilis* | River Bulrush | SciFlu | 144 |
| *Scutellaria lateriflora* | Blue Skullcap | ScuLat | 70 |
| *Setaria viridis* | Green Foxtail | SetVir | 143 |
| *Silene noctiflora* | Night-Flowering Catchfly | SilNoc | 171 |
| *Smilacina stellata* | Star-Flowered Solomon's-Seal | SmiSte | 4 |
| *Smilax herbacea* | Carrionflower | SmiHer | 8 |
| *Solidago canadensis* | Graceful Goldenrod | SolCan | 32 |
| *Sonchus arvensis* | Perennial Sow-Thistle | SonArv | 22 |
| *Spartina pectinata* | Prairie Cord Grass | SpaPec | 174 |
| *Stachys tenuifolia* | Smooth Hedge-Nettle | StaTen | 49 |
| *Stellaria longifolia* | Long-Leaved Stitchwort | SteLon | 168 |
| *Tanacetum vulgare* | Tansy | TanVul | 112 |
| *Taraxicum officinale* | Dandelion | TarOff | 3 |
| *Thalictrum dasycarpum* | Tall Meadow-Rue | ThaDas | 90 |
| *Thalictrum venulosum* | Veiny Meadow-Rue | ThaVen | 11 |
| *Tragopogon dubius* | Yellow Goat's-Beard | TraDub | 155 |
| *Trifolium pratense* | Red Clover | TriPra | 166 |
| *Trifolium repens* | White Clover | TriRep | 101 |
| *Trillium cernuum* | Nodding Trillium | TriCer | 39 |
| *Urtica dioica* | Stinging Nettle | UrtDio | 115 |
| *Vicia americana* | American Vetch | VicAme | 43 |
| *Viola canadensis* | Canada Violet | VioCan | 120 |
| *Viola pubescens* | Downy Yellow Violet | VioPub | 58 |
| *Xanthium strumarium* | Cocklebur | XanStr | 169 |
| *Zizia aurea* | Golden Alexanders | ZizAur | 61 |
| Seed Bank Species | | | |
| *Agrostis scabra* | Rough Hair Grass | AgrSca | 20 |
| *Amaranthus graecizans* | Tumbleweed | AmaGra | 65 |
| *Ambrosia artemisiifolia* | Common Ragweed | AmbArt | 43 |
| *Amphicarpa bracteata* | Hog-Peanut | AmpBra | 44 |
| *Anemone canadensis* | Canada Anemone | AneCan | 13 |
| *Arctium minus* | Lesser Burdock | ArcMin | 23 |
| *Arenaria lateriflora* | Blunt-Leaved Sandwort | AreLat | 66 |
| *Artemisia absinthium* | Absinthe | ArtAbs | 14 |

| Scientific Name | Common Name | Code | Rank |
|---|---|---|---|
| *Brassica campestris* | Bird-Rape | BraCam | 54 |
| *Brassica kaber* | Wild Mustard | BraKab | 35 |
| *Campanula rapunculoides* | Creeping Bluebell | CamRap | 24 |
| *Caragana arborescens* | Common Caragana | CarArb | 55 |
| *Cardamine pensylvania* | Bitter Cress | CardPe | 67 |
| *Carex spp.* | Carex spp. | CarSpp | 4 |
| *Chenopodium album* | Lamb's-Quarters | CheAlb | 40 |
| *Chenopodium glaucum* | Oak-Leaved Goosefoot | CheGla | 30 |
| *Chenopodium hybridum* | Maple-Leaved Goosefoot | CheHyb | 68 |
| *Cirsium arvense* | Canada Thistle | CirArv | 3 |
| *Cornus stolonifera* | Red-Osier Dogwood | CorSto | 32 |
| *Corydalis aurea* | Golden Corydalis | CorAur | 69 |
| *Epilobium glandulosum* | Northern Willowherb | EpiGla | 27 |
| *Equisetum arvense* | Common Horsetail | EquArv | 70 |
| *Erigeron canadensis* | Canada Fleabane | EriCan | 45 |
| *Erysimum cheiranthoides* | Wormseed Mustard | EryChe | 25 |
| *Euphorbia glyptosperma* | Thyme-Leaved Spurge | EupGly | 46 |
| *Galeopsis tetrahit* | Hemp Nettle | GalTet | 56 |
| *Galium triflorum* | Sweet-Scented Bedstraw | GalTri | 8 |
| *Geranium bicknellii* | Bicknell's Cranesbill | GerBic | 71 |
| *Glechoma hederacea* | Ground-Ivy | GleHed | 57 |
| *Hackelia virginiana* | Virginia Stickseed | HacVir | 15 |
| *Hesperis matronalis* | Dame's-Rocket | HesMat | 41 |
| *Juncus tenuis* | Path Rush | JunTen | 72 |
| *Laportea canadensis* | Wood Nettle | LapCan | 73 |
| *Lathyrus ochroleucus* | Cream-Colored Vetchling | LatOch | 47 |
| *Lepidium densiflorum* | Common Peppergrass | LepDen | 36 |
| *Lindernia dubia* | False Pimpernel | LinDub | 74 |
| *Lycopus americana* | Water-Horehound | LycAme | 75 |
| *Lysimachia ciliata* | Fringed Loosestrife | LysCil | 37 |
| *Matricaria maritima* | Scentless Chamomile | MatMar | 58 |
| *Matricaria matricarioides* | Pineappleweed | MatMat | 59 |
| *Medicago lupulina* | Black Medick | MedLup | 19 |
| *Medicago sativa* | Alfalfa | MedSat | 60 |
| *Meehania cordata* | Meehania | MeeCor | 48 |
| *Melilotus alba* | White Sweet-Clover | MelAlb | 26 |
| *Mentha arvensis* | Field Mint | MenArv | 28 |
| *Muhlenbergia racemosa* | Marsh Muhly | MuhRac | 49 |

| Scientific Name | Common Name | Code | Rank |
|---|---|---|---|
| *Oenothera biennis* | Yellow Evening-Primrose | OenBie | 33 |
| *Oxalis europaea* | Yellow Wood-Sorrel | OxaEur | 12 |
| *Panicum capillare* | Witch Grass | PanCap | 38 |
| *Phalaris arundinacea* | Reed Canary Grass | PhaAru | 29 |
| *Plantago major* | Common Plantain | PlaMaj | 42 |
| *Plantago media* | Hoary Plantain | PlaMed | 10 |
| *Poa pratensis* | Kentucky Blue Grass | PoaPra | 1 |
| *Poa palustris* | Fowl Blue Grass | PoaPal | 50 |
| *Polygonum convolvulus* | Wild Buckwheat | PolCon | 61 |
| *Polygonum lapathifolium* | Nodding Smartweed | PolLap | 21 |
| *Polygonum persicaria* | Lady's Thumb | PolPer | 31 |
| *Potentilla norvegica* | Rough Cinquefoil | PotNor | 5 |
| *Ranunculus abortivus* | Smooth-Leaved Buttercup | RanAbo | 17 |
| *Raphanus sativa* | Radish | RapSat | 62 |
| *Ribes americanum* | Wild Black Currant | RibAme | 51 |
| *Rorippa islandica* | Marsh Yellow Cress | RorIsl | 16 |
| *Rubus idaeus* | Wild Red Raspberry | RubIda | 9 |
| *Rumex maritimus* | Golden Dock | RumMar | 22 |
| *Rumex orbiculatus* | Great Water Dock | RumOrb | 76 |
| *Scutellaria lateriflora* | Blue Skullcap | ScuLat | 52 |
| *Senecio vulgaris* | Common Groundsel | SenVul | 63 |
| *Seteria viridis* | Green Foxtail | SetVir | 18 |
| *Solidago canadensis* | Graceful Goldenrod | SolCan | 39 |
| *Sonchus arvensis* | Perennial Sow-Thistle | SonArv | 2 |
| *Stachys tenufolia* | Smooth Hedge-Nettle | StaTen | 77 |
| *Taraxacum officinale* | Dandelion | TarOff | 6 |
| *Thalictrum venulosum* | Veiny Meadow-Rue | ThaVen | 34 |
| *Thlaspi arvense* | Stinkweed | ThlArv | 11 |
| *Trifolium repens* | White Clover | TriRep | 64 |
| *Ulmus americana* | American Elm | UlmAme | 78 |
| *Urtica dioica* | Stinging Nettle | UrtDio | 7 |
| *Verbena bracteata* | Bracted Vervain | VerBra | 79 |
| *Veronica peregrina* | Hairy Speedwell | VerPer | 53 |

# Appendix 3: Disturbance Variables

**Appendix 3**. Measures of disturbance for the 25 study sites.

| Site | Connectivity | A/P | Area (ha) | Disturbance | % Canopy Cover | Garbage |
|---|---|---|---|---|---|---|
| U1 | 1.5 | 13.7 | 0.67 | 8 | 54.6 | 1.8 |
| U2 | 2.5 | 13.4 | 0.30 | 10 | 80.2 | 4.3 |
| U3 | 2.2 | 1.7 | 0.07 | 9 | 67.3 | 5.8 |
| U4 | 3.0 | 15.0 | 0.43 | 10 | 93.1 | 6.3 |
| U5 | 0.0 | 22.9 | 1.03 | 9 | 81.3 | 2.8 |
| S1 | 4.2 | 19.0 | 2.94 | 8 | 75.4 | 1.7 |
| S2 | 7.1 | 39.0 | 10.23 | 7 | 57.7 | 1.2 |
| S3 | 26.4 | 29.0 | 5.08 | 6 | 71.8 | 0.8 |
| S4 | 25.4 | 21.5 | 1.82 | 7 | 72.3 | 0.5 |
| S5 | 37.7 | 32.7 | 3.39 | 6 | 72.3 | 0.0 |
| H1 | 43.3 | 49.1 | 16.03 | 6 | 69.4 | 0.0 |
| H2 | 15.3 | 47.3 | 15.99 | 4 | 66.9 | 0.0 |
| H3 | 208.5 | 34.0 | 4.75 | 3 | 61.5 | 0.0 |
| H4 | 32.1 | 42.9 | 20.89 | 1 | 82.7 | 0.0 |
| H5 | 31.6 | 63.1 | 17.03 | 3 | 67.7 | 0.0 |
| L1 | 8.6 | 36.8 | 9.26 | 5 | 69.1 | 0.0 |
| L2 | 21.6 | 35.8 | 17.53 | 5 | 76.0 | 0.2 |
| L3 | 9.2 | 36.2 | 13.19 | 2 | 75.5 | 0.0 |
| L4 | 33.9 | 51.3 | 11.71 | 1 | 64.5 | 0.0 |
| L5 | 135.3 | 58.3 | 28.64 | 2 | 65.8 | 0.0 |
| R1 | 18.0 | 35.9 | 6.19 | 6 | 75.4 | 0.0 |
| R2 | 703.5 | 78.0 | 62.43 | 4 | 45.1 | 0.0 |
| R3 | 460.5 | 104.7 | 43.95 | 4 | 61.3 | 0.0 |
| R4 | 206.9 | 101.0 | 59.83 | 4 | 66.5 | 0.0 |
| R5 | 19.3 | 69.3 | 63.26 | 2 | 77.5 | 0.0 |

## Appendix 4: Environment Variables

**Appendix 4**. Environment and edaphic variables for the 25 study sites.

| Site | pH | Ec | Topography | Soil Composition by % Sand | Silt | Clay | % Soil Moisture |
|---|---|---|---|---|---|---|---|
| U1 | 8.10 | 0.14 | 2.6 | 28.5 | 47.4 | 26.0 | 21.0 |
| U2 | 8.15 | 0.16 | 2.5 | 17.2 | 53.4 | 31.6 | 18.6 |
| U3 | 8.39 | 0.14 | 2.9 | 32.9 | 41.4 | 27.3 | 16.8 |
| U4 | 7.83 | 0.17 | 2.8 | 22.3 | 50.7 | 28.4 | 22.9 |
| U5 | 8.02 | 0.14 | 2.3 | 21.2 | 52.1 | 27.1 | 20.1 |
| S1 | 7.78 | 0.15 | 2.0 | 33.4 | 47.8 | 19.2 | 25.4 |
| S2 | 7.25 | 0.15 | 2.1 | 30.5 | 41.2 | 26.8 | 24.3 |
| S3 | 7.80 | 0.14 | 2.2 | 28.9 | 49.9 | 22.4 | 25.9 |
| S4 | 7.82 | 0.12 | 2.3 | 32.6 | 46.4 | 20.1 | 21.2 |
| S5 | 7.36 | 0.14 | 1.4 | 25.2 | 41.8 | 31.8 | 22.8 |
| H1 | 6.76 | 0.17 | 1.9 | 20.3 | 39.4 | 38.9 | 25.4 |
| H2 | 7.40 | 0.14 | 2.1 | 32.9 | 46.1 | 22.8 | 24.0 |
| H3 | 7.11 | 0.18 | 1.8 | 29.0 | 48.1 | 24.0 | 25.8 |
| H4 | 7.85 | 0.14 | 1.8 | 19.4 | 56.7 | 24.2 | 23.9 |
| H5 | 7.71 | 0.16 | 1.6 | 25.9 | 52.1 | 19.9 | 26.4 |
| L1 | 6.94 | 0.15 | 1.7 | 29.7 | 46.3 | 24.0 | 26.4 |
| L2 | 7.87 | 0.15 | 2.5 | 12.8 | 59.3 | 30.2 | 24.1 |
| L3 | 7.56 | 0.15 | 1.8 | 24.7 | 51.2 | 22.9 | 22.9 |
| L4 | 7.87 | 0.17 | 2.5 | 11.7 | 59.0 | 29.4 | 24.7 |
| L5 | 7.92 | 0.13 | 2.2 | 10.4 | 63.2 | 25.4 | 24.3 |
| R1 | 7.63 | 0.16 | 2.2 | 29.9 | 52.3 | 16.3 | 25.9 |
| R2 | 7.07 | 0.17 | 1.8 | 26.9 | 46.8 | 26.7 | 24.4 |
| R3 | 7.29 | 0.15 | 2.3 | 25.8 | 46.3 | 27.6 | 25.0 |
| R4 | 7.23 | 0.14 | 1.7 | 28.7 | 47.3 | 23.9 | 23.1 |
| R5 | 7.91 | 0.13 | 2.2 | 16.7 | 58.4 | 24.5 | 23.4 |

## Appendix 5: Generalist Species

**Appendix 5**. Characterization of generalist plant species, classified according to their vulnerable or opportunistic response to disturbance.

| Species and grouping by | | | | Guilds# | | | | Occurrence rank†† | | |
|---|---|---|---|---|---|---|---|---|---|---|
| V:O ratio | V:O† | VI‡ | OI§ | Or | Lf | Ph | Dt | Tot | Cy | NCy |
| **VI3 (2 < V:O < 5)** | | | | | | | | | | |
| *Menispermum canadense* | 4.94 | 5.00 | 0.21 | N | W | S | END | 34 | 55 | 28 |
| *Geum aleppicum* | 3.64 | 4.00 | 0.37 | N | PF | S | EPI | 97 | 107 | 82 |
| *Equisetum hymale* | 3.33 | 4.00 | 0.50 | N | PF | E | ANE | 66 | 115 | 53 |
| *Galeopsis tetrahit* | 3.33 | 4.00 | 0.50 | E | AF | S | END | 111 | 112 | 98 |
| *Galium triflorum* | 3.28 | 3.33 | 0.32 | N | PF | S | END | 13 | 97 | 3 |
| *Elymus virginicus* | 2.99 | 3.33 | 0.45 | N | PG | F | ANE | 56 | 87 | 50 |
| *Lathyrus palustris* | 2.67 | 3.00 | 0.50 | N | PF | S | AUT | 101 | 99 | 96 |
| *Thalictrum dasycarpum* | 2.50 | 3.00 | 0.60 | N | PF | S | EPI | 91 | 109 | 73 |
| *Apocynum androsaemifolium* | 2.44 | 2.67 | 0.50 | N | PF | S | ANE | 44 | 34 | 49 |
| *Laportea canadensis* | 2.44 | 2.67 | 0.50 | N | PF | S | ANE | 43 | 43 | 40 |
| *Carex peckii* | 2.39 | 2.50 | 0.46 | N | PG | S | BAR | 27 | 37 | 24 |
| *Oxalis europaea* | 2.39 | 2.50 | 0.46 | N | PF | S | AUT | 54 | 73 | 48 |
| *Lathyrus ochroleucus* | 2.33 | 2.50 | 0.50 | N | PF | S | AUT | 52 | 66 | 44 |
| *Glycyrrhiza lepidota* | 2.31 | 2.00 | 0.30 | N | PF | S | EPI | 83 | 98 | 66 |
| *Vitis riparia* | 2.26 | 2.50 | 0.55 | N | W | S | END | 31 | 47 | 25 |
| *Arenaria lateriflora* | 2.18 | 2.00 | 0.37 | N | PF | S | ANE | 63 | 93 | 54 |
| *Carex cristatella* | 2.18 | 2.00 | 0.37 | N | PG | F | BAR | 108 | 113 | 93 |
| *Crataegus crysocarpa* | 2.13 | 2.00 | 0.41 | N | W | E | END | 48 | 50 | 43 |
| *Maianthemum canadense* | 2.00 | 2.00 | 0.50 | N | PF | E | END | 11 | 16 | 7 |
| *Carex pensylvanica* | 2.00 | 3.00 | 1.00 | N | PG | E | BAR | 77 | 69 | 78 |
| *Tanacetum vulgare* | 2.00 | 2.00 | 0.50 | E | PF | F | ANE | 112 | 104 | 100 |
| **VI4 (1 < V:O < 2)** | | | | | | | | | | |
| *Rhus radicans* | 1.95 | 2.00 | 0.54 | N | W | S | END | 6 | 9 | 6 |
| *Solidago canadensis* | 1.90 | 2.00 | 0.58 | N | PF | F | ANE | 32 | 33 | 33 |
| *Rubus pubescens* | 1.87 | 2.00 | 0.60 | N | PF | S | END | 75 | 74 | 70 |
| *Heracleum lanatum* | 1.71 | 2.00 | 0.75 | N | PF | S | END | 90 | 84 | 80 |
| *Lathyrus venosus* | 1.71 | 2.00 | 0.75 | N | PF | S | AUT | 95 | 77 | 99 |
| *Anemone canadensis* | 1.69 | 1.60 | 0.54 | N | PF | S | ANE | 29 | 54 | 22 |
| *Amphicarpa bracteata* | 1.67 | 1.67 | 0.60 | N | PF | F | END | 15 | 26 | 13 |
| *Smilax herbacea* | 1.67 | 1.67 | 0.60 | N | PF | E | END | 10 | 21 | 4 |
| *Actaea rubra* | 1.62 | 1.50 | 0.55 | N | PF | E | END | 51 | 36 | 56 |

| Species and grouping by V:O ratio | | | | Guilds# | | | | Occurrence rank†† | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | V:O† | VI‡ | OI§ | Or | Lf | Ph | Dt | Tot | Cy | NCy |
| *Galium boreale* | 1.62 | 1.50 | 0.55 | N | PF | S | END | 36 | 29 | 41 |
| *Amelanchier alnifolia* | 1.58 | 1.67 | 0.69 | N | W | E | END | 23 | 13 | 31 |
| *Tilia americana* | 1.58 | 1.67 | 0.69 | N | W | E | ANE | 14 | 20 | 14 |
| *Trillium cernuum* | 1.56 | 1.50 | 0.60 | N | PF | E | MYR | 39 | 45 | 39 |
| *Aralia nudicaulis* | 1.47 | 1.67 | 0.82 | N | PF | S | END | 17 | 14 | 17 |
| *Populus tremuloides* | 1.43 | 1.50 | 0.75 | N | W | E | ANE | 65 | 58 | 64 |
| *Sonchus arvensis* | 1.43 | 1.43 | 0.70 | E | PF | F | ANE | 22 | 41 | 16 |
| *Thalictrum venulosum* | 1.43 | 1.43 | 0.70 | N | PF | S | EPI | 12 | 19 | 9 |
| *Sanicula marilandica* | 1.35 | 1.50 | 0.86 | N | PF | S | EPI | 58 | 39 | 71 |
| *Lonicera dioica* | 1.34 | 1.60 | 0.94 | N | W | E | END | 57 | 35 | 75 |
| *Corylus cornuta* | 1.33 | 1.67 | 1.00 | N | W | E | END | 40 | 30 | 45 |
| *Fragaria virginiana* | 1.33 | 1.33 | 0.75 | N | PF | S | END | 73 | 51 | 95 |
| *Viola pubescens* | 1.26 | 1.20 | 0.75 | N | PF | E | MYR | 59 | 48 | 59 |
| *Zizia aurea* | 1.26 | 1.60 | 1.07 | N | PF | E | EPI | 62 | 49 | 61 |
| *Ribes americanum* | 1.25 | 1.25 | 0.80 | N | W | E | END | 28 | 22 | 35 |
| *Carex deweyana* | 1.23 | 1.33 | 0.90 | N | PG | S | BAR | 46 | 32 | 51 |
| *Oryzopsis asperifolia* | 1.23 | 1.33 | 0.90 | N | PG | E | EPI | 70 | 70 | 69 |
| *Prunus virginiana* | 1.21 | 1.25 | 0.86 | N | W | E | END | 18 | 8 | 27 |
| *Symphoricarpos occidentalis* | 1.21 | 1.25 | 0.86 | N | W | S | END | 7 | 10 | 8 |
| *Melilotus alba* | 1.20 | 1.00 | 0.67 | E | AF | S | END | 61 | 63 | 55 |
| *Viburnum opulus* | 1.20 | 1.20 | 0.83 | N | W | S | END | 64 | 52 | 67 |
| *Rosa acicularis* | 1.18 | 1.00 | 0.69 | N | W | S | END | 26 | 31 | 23 |
| *Asclepias ovalifolia* | 1.14 | 1.00 | 0.75 | N | PF | S | ANE | 105 | 94 | 102 |
| *Poa pratense* | 1.11 | 1.11 | 0.90 | E | PG | S | END | 5 | 11 | 5 |
| *Quercus macrocarpa* | 1.11 | 1.11 | 0.90 | N | W | E | END | 19 | 18 | 21 |
| *Smilacina stellata* | 1.11 | 1.11 | 0.90 | N | PF | S | END | 4 | 4 | 12 |
| *Bidens frondosa* | 1.10 | 1.33 | 1.12 | N | AF | F | EPI | 94 | 90 | 86 |
| *Bromus inermis* | 1.08 | 1.00 | 0.86 | E | PG | S | END | 8 | 7 | 11 |
| *Celastrus scandens* | 1.08 | 1.00 | 0.86 | N | W | S | END | 85 | 64 | 94 |
| *Vicia americana* | 1.08 | 1.00 | 0.86 | N | PF | S | END | 45 | 40 | 42 |
| *Cornus stolonifera* | 1.07 | 1.11 | 0.96 | N | W | S | END | 21 | 24 | 20 |
| *Viburnum lentago* | 1.07 | 0.80 | 0.68 | N | W | S | END | 60 | 53 | 58 |
| *Equisetum arvense* | 1.05 | 1.14 | 1.05 | N | PF | E | ANE | 33 | 42 | 26 |
| *Osmorhiza longistylis* | 1.05 | 1.00 | 0.90 | N | PF | E | EPI | 42 | 28 | 52 |
| *Cirsium arvense* | 1.04 | 1.00 | 0.92 | E | PF | F | ANE | 20 | 25 | 18 |
| *Viburnum rafinesquianum* | 1.02 | 1.33 | 1.29 | N | W | S | END | 30 | 15 | 46 |

| Species and grouping by V:O ratio | V:O† | VI‡ | OI§ | Guilds# Or | Lf | Ph | Dt | Occurrence rank†† Tot | Cy | NCy |
|---|---|---|---|---|---|---|---|---|---|---|
| **Generalists (V:O = 1)** | | | | | | | | | | |
| *Acer negundo* | 1.00 | 1.00 | 1.00 | N | W | E | ANE | 2 | 5 | 2 |
| *Agropyron trachycaulum* | 1.00 | 1.00 | 1.00 | N | PG | S | END | 35 | 38 | 37 |
| *Aster ciliolatus* | 1.00 | 1.50 | 1.50 | N | PF | F | ANE | 69 | 60 | 81 |
| *Botrychium virginianum* | 1.00 | 0.00 | 0.00 | N | PF | S | ANE | 107 | - | 90 |
| *Fraxinus pennsylvanica* | 1.00 | 1.00 | 1.00 | N | W | S | ANE | 1 | 6 | 1 |
| *Potentilla norvegica* | 1.00 | 0.00 | 0.00 | N | AF | F | END | 126 | - | 117 |
| *Prunus nigra* | 1.00 | 1.00 | 1.00 | N | W | E | END | 116 | 101 | 108 |
| *Ulmus americana* | 1.00 | 1.00 | 1.00 | N | W | E | ANE | 16 | 17 | 15 |
| **OI3 (0.5 < V:O < 1)** | | | | | | | | | | |
| *Parthenocissus quinquefolia* | 0.99 | 1.11 | 1.12 | N | W | S | END | 9 | 1 | 19 |
| *Taraxicum officinale* | 0.96 | 0.89 | 0.96 | E | PF | E | ANE | 3 | 2 | 10 |
| *Lysimachia ciliata* | 0.95 | 0.67 | 0.75 | N | PF | S | ANE | 84 | 62 | 97 |
| *Polygonatum biflorum* | 0.91 | 1.00 | 1.20 | N | PF | E | END | 79 | 65 | 84 |
| *Arctium minor* | 0.88 | 0.75 | 1.00 | E | BF | F | EPI | 25 | 12 | 36 |
| *Plantago media* | 0.86 | 0.86 | 1.17 | E | PF | F | END | 49 | 27 | 68 |
| *Lycopus americana* | 0.80 | 1.00 | 1.50 | N | PF | F | BAR | 115 | 100 | 107 |
| *Poa palustris* | 0.78 | 0.67 | 1.12 | N | PG | S | END | 96 | 85 | 92 |
| *Asparagus officinalis* | 0.67 | 0.00 | 0.50 | E | PF | S | END | 100 | 80 | 103 |
| *Melilotus officinalis* | 0.67 | 0.67 | 1.50 | E | AF | S | END | 113 | 88 | 110 |
| *Medicago lupulina* | 0.63 | 0.33 | 1.12 | E | AF | S | END | 78 | 72 | 77 |
| *Hackelia virginiana* | 0.57 | 0.57 | 1.75 | N | BF | S | EPI | 68 | 59 | 79 |
| *Prunus americana* | 0.57 | 0.00 | 0.75 | N | W | E | END | 88 | 71 | 87 |

† Ratio of vulnerability over opportunism.

‡ Vulnerability idex, defined as the proportion of reference sites (N = 5) in which a species occurred, divided by the proportion of city sites (N = 10) in which a species occurred.

§ Opportunism index defined as the proportion of city sites (N = 10) in which a species occurred, divided b; the proportion of non-city sites (N = 15) in which a species occurred.

# Functional Guilds: Or, origin (E - exotic, N - native); Lf, plant lifeform (AG - annual graminoid, PG - perrenial graminoid, AF - annual forb, BF - biennial forb, PF - perrenial forb, W- woody); Ph, flowering phenology (E - ephemeral herbs flowering March - May, S - summer herbs flowering June - August, F - fall herbs flowering September - November); Dt, dispersal type (ANE - anemochore wind-dispersed, AUT - autochore e dispersed, BAR - barichore gravity-dispersed, END - endozoochore animal-consumed, EPI - epizoochore animal-carried, MYR - myrmecochore ant-dispersed).

†† Proportional occurrence of each species ranked in decreasing occurrence from most frequent (1) based on: Tot - all species (N = 126); Cy - species in city sites (N = 117); NCy - species in non-city sites (N = 119).

# Appendix 6:Diversity Correlation

**Appendix 6**. Correlation of indicator species with richness ($N_0$) and dominance ($N_2$) of exotic, native, vulnerable, opportunistic, and overall species.

| | $N_2$ | | | $N_0$ | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | Exotic | Native | Total | Exotic | Native | Total | Vuln-erable | Oppor-tunist |
| *Arctium minor* | 0.02 NS | -0.41 * | -0.40 * | 0.36 NS | -0.63 *** | -0.57 ** | -0.22 NS | 0.32 NS |
| *Artemisia absinthium* | 0.11 NS | -0.19 NS | -0.14 NS | 0.51 ** | -0.38 NS | -0.27 NS | -0.18 NS | 0.44 * |
| *Caragana arborescens* | 0.48 * | 0.11 NS | 0.27 NS | 0.20 NS | 0.15 NS | 0.20 NS | -0.21 NS | 0.32 NS |
| *Chenopodium album* | -0.17 NS | -0.23 NS | -0.22 NS | 0.28 NS | -0.46 * | -0.41 * | -0.30 NS | 0.37 NS |
| *Convolvulus sepium* | 0.03 NS | 0.45 * | 0.43 * | -0.06 NS | 0.50 * | 0.49 * | 0.50 * | -0.14 NS |
| *Cotoneaster melanocarpa* | 0.41 * | -0.02 NS | 0.12 NS | 0.25 NS | 0.33 NS | 0.40 * | 0.03 NS | 0.35 NS |
| *Glechoma hederacea* | 0.03 NS | -0.14 NS | -0.07 NS | 0.63 *** | -0.44 * | -0.31 NS | -0.25 NS | 0.50 ** |
| *Hesperis matronalis* | 0.08 NS | -0.42 * | -0.32 NS | 0.36 NS | -0.55 ** | -0.48 * | -0.35 NS | 0.35 NS |
| *Lonicera tartarica* | 0.45 * | -0.35 NS | -0.11 NS | 0.41 * | -0.26 NS | -0.17 NS | -0.61 *** | 0.72 *** |
| *Plantago major* | 0.30 NS | 0.22 NS | 0.40 * | 0.53 ** | 0.25 NS | 0.37 NS | 0.06 NS | 0.53 ** |
| *Rhamnus cathartica* | 0.18 NS | -0.36 NS | -0.20 NS | 0.23 NS | -0.08 NS | -0.03 NS | -0.50 * | 0.46 * |
| *Rumex crispus* | 0.26 NS | -0.36 NS | -0.23 NS | 0.50 * | -0.50 * | -0.40 * | -0.33 NS | 0.43 * |
| *Setaria viridis* | -0.12 NS | -0.35 NS | -0.31 NS | 0.16 NS | -0.51 ** | -0.49 * | -0.39 NS | 0.39 NS |
| *Solanum dulcamara* | 0.19 NS | -0.56 ** | -0.46 * | 0.30 NS | -0.78 *** | -0.73 *** | -0.46 * | 0.41 * |
| *Sonchus arvensis* | -0.09 NS | 0.65 *** | 0.62 *** | 0.22 NS | 0.62 *** | 0.68 *** | 0.57 ** | -0.08 NS |
| *Trifolium repens* | 0.13 NS | -0.11 NS | 0.04 NS | 0.74 *** | -0.10 NS | 0.06 NS | 0.01 NS | 0.64 *** |
| *Urtica dioica* | 0.06 NS | -0.36 NS | -0.35 NS | 0.23 NS | -0.61 *** | -0.57 ** | -0.29 NS | 0.31 NS |
| *Anemone canadensis* | -0.25 NS | 0.56 ** | 0.58 ** | -0.15 NS | 0.51 ** | 0.49 * | 0.57 ** | -0.41 * |
| *Amelanchier alnifolia* | 0.12 NS | 0.25 NS | 0.38 NS | 0.12 NS | 0.51 ** | 0.54 ** | -0.16 NS | 0.25 NS |
| *Apocynum cannabinum* | -0.01 NS | 0.39 NS | 0.50 * | -0.03 NS | 0.48 * | 0.48 * | 0.55 ** | -0.23 NS |
| *Aster simplex* | -0.16 NS | 0.40 * | 0.35 NS | -0.12 NS | 0.42 * | 0.40 * | 0.76 *** | -0.55 ** |
| *Carex aquatilis* | -0.05 NS | 0.15 NS | 0.12 NS | 0.08 NS | 0.54 ** | 0.57 ** | 0.68 *** | -0.16 NS |
| *Carex sprengelii* | 0.28 NS | 0.17 NS | 0.17 NS | -0.04 NS | 0.28 NS | 0.28 NS | 0.41 * | -0.14 NS |
| *Carex* spp. † | -0.17 NS | 0.55 ** | 0.49 * | -0.33 NS | 0.82 *** | 0.77 *** | 0.43 * | -0.39 NS |
| *Chenopodium hybridum* | -0.12 NS | -0.35 NS | -0.31 NS | 0.16 NS | -0.51 ** | -0.49 * | -0.39 NS | 0.39 NS |
| *Crataegus crysocarpa* | 0.13 NS | 0.50 * | 0.58 ** | 0.04 NS | 0.53 ** | 0.55 ** | 0.30 NS | -0.02 NS |
| *Elymus canadensis* | 0.21 NS | 0.04 NS | 0.16 NS | 0.42 * | 0.11 NS | 0.20 NS | -0.09 NS | 0.35 NS |

| | $N_2$ | | | $N_0$ | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | Exotic | Native | Total | Exotic | Native | Total | Vulnerable | Opportunist |
| *Fraxinus pennsylvanica* | -0.16 $^{NS}$ | 0.50 $^{*}$ | 0.45 $^{*}$ | -0.26 $^{NS}$ | 0.50 $^{*}$ | 0.45 $^{*}$ | 0.58 $^{**}$ | -0.51 $^{**}$ |
| *Galium boreale* | 0.35 $^{NS}$ | 0.38 $^{NS}$ | 0.53 $^{**}$ | 0.15 $^{NS}$ | 0.46 $^{*}$ | 0.50 $^{*}$ | 0.02 $^{NS}$ | 0.19 $^{NS}$ |
| *Galium triflorum* | -0.21 $^{NS}$ | 0.41 $^{*}$ | 0.34 $^{NS}$ | -0.21 $^{NS}$ | 0.40 $^{*}$ | 0.37 $^{NS}$ | 0.64 $^{***}$ | -0.52 $^{**}$ |
| *Helianthus tuberosus* | -0.03 $^{NS}$ | 0.29 $^{NS}$ | 0.30 $^{NS}$ | -0.31 $^{NS}$ | 0.33 $^{NS}$ | 0.27 $^{NS}$ | 0.44 $^{*}$ | -0.37 $^{NS}$ |
| *Lathyrus palustris* | 0.02 $^{NS}$ | 0.40 $^{*}$ | 0.40 $^{*}$ | -0.06 $^{NS}$ | 0.49 $^{*}$ | 0.49 $^{*}$ | 0.41 $^{*}$ | -0.08 $^{NS}$ |
| Matteuccia *struthiopteris* | -0.11 $^{NS}$ | 0.00 $^{NS}$ | -0.13 $^{NS}$ | -0.24 $^{NS}$ | 0.35 $^{NS}$ | 0.30 $^{NS}$ | 0.55 $^{**}$ | -0.45 $^{*}$ |
| *Mentha arvensis* | -0.21 $^{NS}$ | 0.15 $^{NS}$ | -0.03 $^{NS}$ | -0.18 $^{NS}$ | 0.26 $^{NS}$ | 0.22 $^{NS}$ | 0.55 $^{**}$ | -0.33 $^{NS}$ |
| *Phalaris arundinacea* | 0.11 $^{NS}$ | 0.06 $^{NS}$ | 0.09 $^{NS}$ | -0.08 $^{NS}$ | 0.51 $^{**}$ | 0.50 $^{**}$ | 0.77 $^{***}$ | -0.32 $^{NS}$ |
| *Polygonum coccineum* | -0.11 $^{NS}$ | 0.06 $^{NS}$ | 0.01 $^{NS}$ | -0.22 $^{NS}$ | 0.33 $^{NS}$ | 0.29 $^{NS}$ | 0.53 $^{**}$ | -0.34 $^{NS}$ |
| *Ranunculus abortivus* | -0.23 $^{NS}$ | 0.00 $^{NS}$ | -0.11 $^{NS}$ | -0.04 $^{NS}$ | 0.28 $^{NS}$ | 0.28 $^{NS}$ | 0.62 $^{***}$ | -0.30 $^{NS}$ |
| *Rubus idaeus* | -0.20 $^{NS}$ | 0.38 $^{NS}$ | 0.26 $^{NS}$ | -0.06 $^{NS}$ | 0.41 $^{*}$ | 0.40 $^{*}$ | 0.73 $^{***}$ | -0.44 $^{*}$ |
| *Salix interior* | 0.33 $^{NS}$ | -0.08 $^{NS}$ | 0.00 $^{NS}$ | -0.04 $^{NS}$ | 0.35 $^{NS}$ | 0.35 $^{NS}$ | 0.54 $^{**}$ | -0.15 $^{NS}$ |
| *Scirpus fluviatilis* | -0.16 $^{NS}$ | 0.20 $^{NS}$ | 0.04 $^{NS}$ | -0.22 $^{NS}$ | 0.24 $^{NS}$ | 0.20 $^{NS}$ | 0.42 $^{*}$ | -0.32 $^{NS}$ |
| *Scutellaria lateriflora* | -0.25 $^{NS}$ | 0.23 $^{NS}$ | 0.06 $^{NS}$ | 0.06 $^{NS}$ | 0.22 $^{NS}$ | 0.24 $^{NS}$ | 0.51 $^{**}$ | -0.20 $^{NS}$ |
| *Smilax herbacea* | -0.18 $^{NS}$ | 0.58 $^{**}$ | 0.46 $^{*}$ | -0.32 $^{NS}$ | 0.68 $^{***}$ | 0.63 $^{***}$ | 0.38 $^{NS}$ | -0.48 $^{*}$ |
| *Stachys tenuifolia* | -0.43 $^{*}$ | 0.45 $^{*}$ | 0.22 $^{NS}$ | -0.16 $^{NS}$ | 0.46 $^{*}$ | 0.44 $^{*}$ | 0.75 $^{***}$ | -0.45 $^{*}$ |
| *Symphoricarpos occidentalis* | -0.11 $^{NS}$ | 0.45 $^{*}$ | 0.40 $^{*}$ | -0.14 $^{NS}$ | 0.57 $^{**}$ | 0.55 $^{**}$ | 0.21 $^{NS}$ | -0.20 $^{NS}$ |
| *Thalictrum venulosum* | -0.23 $^{NS}$ | 0.73 $^{***}$ | 0.70 $^{***}$ | -0.28 $^{NS}$ | 0.74 $^{***}$ | 0.69 $^{***}$ | 0.41 $^{*}$ | -0.33 $^{NS}$ |
| *Viburnum rafinesquianum* | 0.23 $^{NS}$ | 0.26 $^{NS}$ | 0.40 $^{*}$ | 0.12 $^{NS}$ | 0.41 $^{*}$ | 0.44 $^{*}$ | -0.18 $^{NS}$ | 0.29 $^{NS}$ |
| *Viola canadensis* | 0.19 $^{NS}$ | 0.33 $^{NS}$ | 0.47 $^{*}$ | 0.24 $^{NS}$ | 0.29 $^{NS}$ | 0.35 $^{NS}$ | -0.04 $^{NS}$ | 0.42 $^{*}$ |
| *Zizia aurea* | 0.09 $^{NS}$ | 0.39 $^{NS}$ | 0.47 $^{*}$ | 0.03 $^{NS}$ | 0.36 $^{NS}$ | 0.37 $^{NS}$ | -0.13 $^{NS}$ | 0.15 $^{NS}$ |

* $P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS - not significant $P > 0.05$.

† Includes all *Carex* species grouped together.