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Ecology and management of riparian zone vegetation along small coldwater streams in Northwestern Ontario

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Ecology and Management of Riparian Zone Vegetation Along Small Coldwater Streams in Northwestern Ontario

by

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Masters Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science in Biology

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Abstract

This thesis synthesizes three papers on the ecology of the riparian zone vegetation found along small coldwater streams in northwestern Ontario. The objectives of this thesis were 1) to describe the biodiversity and distribution and abundance of riparian zone plant species and vegetation types along the longitudinal and lateral gradients, 2) to evaluate the current buffer zone guidelines by comparing the riparian plant community between undisturbed sites and sites with adjacent clearcuts and forest fire, and 3) to examine the changes in the plant community trait structure found over the riparian-upland ecotone.

1) The riparian zones of these streams are diverse, with a large proportion of the regional flora, including some locally rare species, represented. The vegetation is predominantly either an *Alnus incana*-dominated swamp thicket or a *Calamagrostis canadensis* and *Carex aquatilis*-dominated meadow marsh. Variation along the longitudinal gradient is weak with few species distributions significantly related to watershed size. Meadow marsh vegetation, however, is concentrated in watersheds 1000ha in area and smaller, likely due to the preference of beaver for streams of those sizes for dam construction. The riparian vegetation is remarkably homogenous along the lateral gradient. There are no distinct vegetation bands within the riparian zone, though some riparian-specialist species are more abundant near the streambank and some upland species are more common near the riparian-upland ecotone. The shoreward extent of the riparian zone, the riparian-upland ecotone, is marked by a strong shift in species composition at the limit of flooding and saturated soils.

2) Riparian plant community composition was compared between sites that were undisturbed, sites where clear-cuts were separated from the riparian zone by a buffer of upland forest, and sites where a forest fire had burned to the riparian zone-upland ecotone. No significant differences in the overall abundance and distribution of species in the riparian vegetation were found between the three disturbance classes, though a small number of species appeared to increase in abundance at burn sites.

These results demonstrate that disturbances in the upland forest do not seriously impact the riparian zone plant community, likely because the riparian species are adapted to a high-light environment and flooding disturbance. The environmental factors that increase in the riparian zone following removal of the adjacent canopy, including light levels, temperature, and wind penetration, do not appear to have a significant influence on the riparian zone vegetation. These results suggest that aspects of the current riparian management guidelines in northwestern Ontario may need to be re-evaluated.

3) The changes in importance of a range of reproductive, physiological, and morphological plant traits were examined over the riparian-upland ecotone. Traits with especially striking changes over the ecotone included leaf type, pollination and dispersal vector, clonal growth form, and a persistent seed bank. These trait patterns were used to generate hypotheses of potential functional explanations for the changes in plant community structure across the ecotone. These results have significance for ecotone theory as they demonstrate that plant traits can have very similar patterns of change across ecotones to those observed for the abundance of many species. Relationships between traits that represent potential functional relationships or trade-offs are identified. Finally, this analysis has some implications for the types of traits that should be included in further trait-matrix studies.

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Many people have generously given their time and energy to help me along the way. Dr. Rob Mackereth provided statistical advice and field support and reviewed the thesis. Dr. Rob Rempel and Dr. John Richardson reviewed the thesis. Darren McCormick provided maps and directions to study sites, produced the map in figure 2, and gave us a tow from that ditch. Bruce Thacker provided logistical and field support. Katherine Stewart and many of the CAEP summer staff assisted in the field. Erika North and the Claude Garton Herbarium provided much good advice and many resources, helping in the identification and preservation of my voucher specimens. Many good discussions (and pints) with Steve Hill, Katherine Stewart, and Robin Bloom have helped me to bring my ideas together. Eleanor Maunula kept everything organized. To all of these people and to any that I have left out - a huge thank you.

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General Introduction

Riparian zones are an important and conspicuous element of the natural landscape. They include the narrow strips of distinctive vegetation found alongside freshwater streams of all sizes, from tiny headwater streamlets to large rivers. The riparian zone has long interested plant ecologists because of the high biodiversity, steep environmental gradients, and abrupt ecotones (e.g. Gregory *et al.* 1991; Malanson 1993; Bendix 1994b; Naiman and Décamps 1997). Land managers and fisheries biologists are interested in riparian zones because of the important ecological services that they provide, especially the maintenance of high water quality and good fish habitat (Gregory *et al.* 1991; Naiman and Décamps 1997). A large fraction of the world's human population lives in riparian zones; the high agricultural productivity and recreational, aesthetic, and economic values makes these habitats of interest to society in general. Worldwide, the ecology of riparian zones and the effective management of riparian zone vegetation are major conservation concerns.

The riparian zones of small headwater streams are found throughout the landscape of northwestern Ontario. Networks of the distinctive thickets of Alder (*Alnus incana*) and the wide wet grass and sedge meadows of the riparian zones are spread throughout the boreal mixedwood forests of the region. Many of these streams support important fish populations and a wide range of mammals, amphibians, and birds. The ecology and management of these unique habitats is a major concern of those responsible for managing the forests and fisheries of northwestern Ontario (Ontario Ministry of Natural Resources 1988; Pike and Racey 1989).

For all of their importance, relatively little is known about the ecology of northwestern Ontario riparian zones. Many studies of riparian plant ecology have been carried out, but they have typically been focussed on larger streams in temperate regions (e.g. Lindsay *et al.* 1961; Osterkamp and Hupp 1984; van Coller *et al.* 2000). The few boreal riparian studies have focussed on larger rivers in the north (e.g. Nanson and Beach 1977; Farjon and Bogaers 1985; Gould and Walker 1999); thus, there is a lack of information on the riparian zones of small streams in the southern boreal forest. Basic information, such as the biodiversity and distribution of vascular plant species within the riparian zone, is lacking. This information gap extends to the management practices used to protect riparian zones in northwestern Ontario. Though buffer zones are commonly used to protect riparian zones and streams from nearby human disruptions (e.g. Clinnick 1985; Ontario Ministry of Natural Resources 1988; Norris 1993), very few studies have reported the effects of such practices on the riparian zone vegetation and its ability to protect the stream. From an ecological perspective, the riparian zone is a very abrupt ecotone separating the aquatic community from the upland forest. Ecotones are well known for the high species diversity and diverse ecological function and community structure that they support in a relatively small portion of the landscape (Weins *et al.* 1985; Delcourt and Delcourt 1992; Lachavanne 1997; Lloyd *et al.* 2000). However, the characteristics of this ecotone, one of the most important landscape features in the boreal forest, are very poorly understood. Without a thorough understanding of the changes in community structure found across this ecotone, it is difficult to develop management strategies tailored to the ecological reality.

This thesis is an exploration of some aspects of the ecology of the riparian zone vegetation of small coldwater streams in northwestern Ontario. Gaps in the basic data on species distribution and abundance will be addressed, along with an evaluation of aspects of the current management approach. Finally, aspects of the shift in community structure at the riparian-upland ecotone will be investigated. The specific questions to be addressed in the three chapters of this thesis are:

1) What is the vascular plant biodiversity of these riparian zones, and how are these species distributed with respect to watershed size and lateral proximity to the stream? The biodiversity, distribution, and abundance data will provide the baseline data necessary to evaluate and interpret the results of the subsequent chapters.
2) What change(s) in the riparian zone plant community follow clearcutting and the creation of a buffer zone, or a forest fire adjacent to the stream? This chapter will test the effectiveness of the current buffer zone regulations in preventing detrimental changes in the riparian plant community following

logging, and will compare that response to the response following a forest fire, a canopy-destroying disturbance that does not leave a buffer zone.

3) What changes in plant community structure occur at the riparian zone-upland ecotone? This chapter will use a trait matrix approach to identify the aspects of plant community structure which change most strongly at the ecotone. This will help identify the important environmental factors contributing to structuring the riparian zone vegetation.

The introductory sections of this thesis will present some background information including a discussion of the appropriate working definition of the riparian zone, and a brief literature review on the ecology of riparian zone plants and current riparian management practices. This section will be followed by a description of the study area, and the field and statistical methodologies used. At the core of the thesis are three chapters that address the above objectives. Finally, a general discussion is presented.

Literature Review

Definition of the Riparian Zone

"Riparian" is a word meaning "of, or on a river bank" from the Latin *riparius*, or "bank" (Fowler and Fowler 1964). From this root, the term "riparian zone" has come to be applied to a broad class of in- and near-stream communities and structures. Numerous working definitions of the riparian zone have been developed (Gregory *et al.* 1991; Ilhardt *et al.* 2000). The term has been given such a wide array of meanings that in practice it has lost much of its use as a technical term, beyond indicating that something is near a stream. Bren (1993), for example, defined the riparian zone simply as an area of land near a stream that is significantly influenced by that close association. Naiman and Décamps (1997) incorporated much more detail when they defined the riparian zone as including "the stream channel between the low and high water marks and that portion of the terrestrial landscape from the high water mark toward the uplands where vegetation may be influenced by elevated water tables or flooding and by the ability of soils to hold water". Essentially, a riparian zone is a wetland, or an area of the landscape transitional between the aquatic and terrestrial systems where saturated soils or periodic flooding have a dominant influence on the soil and plant community development (Cowarden *et al.* 1979). Naiman and Décamps' (1997) working definition of the riparian zone will be followed in this thesis.

Ecological Services

Riparian zones provide a range of ecological services (Ehrlich and Wilson 1991) to the wider landscape due to their position at the interface between the terrestrial and aquatic environments. The primary ecological services that riparian zones provide can be grouped into four general categories: filtering and buffering, inputs of organic matter, centers of biodiversity, and stream bank protection (Gregory *et al.* 1991; Malanson 1993; Naiman and Décamps 1997). The function of riparian zones as landscape corridors may also be important but is still subject to debate (Naiman and Décamps 1997).

Filtering and Buffering

Riparian zones serve as important filters and buffers of groundwater and surface runoff water before it enters the stream. This function is critical for maintaining stream water quality, especially if the upland is disturbed by human activity (Binkley and Brown 1993; Malanson 1993; Naiman and Décamps 1997). The riparian vegetation absorbs water from shallow groundwater flows and utilizes some of the dissolved nutrients carried by it. The vegetation also forms a physical barrier that slows the movement of fine sediments in surface runoff into the stream. These sediments, especially runoff from agricultural fields, can contain high concentrations of absorbed nutrients. Large quantities of these nutrients can be taken up by the plants of the riparian zone and sequestered there (e.g. Peterjohn and Correll 1984; Osborne and Kovacic 1993). It is not clear whether riparian zones are nutrient sinks over the long term, but over the short term, especially during flood events, uptake of nutrients by riparian plants exceeds inputs to the stream (Malanson 1993; Osborne and Kovacic 1993). The short-term accumulation of nutrients in plant biomass may spread out inputs of nutrients to the water over time (Naiman and Décamps 1997). In a forestry context suspended sediments washed from clearcuts and particularly from logging roads can be very detrimental to water quality and fish populations (Binkley and Brown 1993). Riparian zone vegetation forms a physical barrier to these sediment flows, trapping much of it before it can enter the stream (e.g. Trimble and Sartz 1957; Binkley and Brown 1993; Naiman and Décamps 1997).

Organic Matter Inputs

Inputs of fine organic materials from the riparian zone into the stream form the basis of the food chain within the stream (Hynes 1975; Vannote *et al.* 1980; Minshall *et al.* 1985; Naiman *et al.* 1987; Malanson 1993; Naiman and Décamps 1997; Meyer and Wallace 2001). The largest inputs of organic materials occur in low-order headwater streams (Naiman *et al.* 1987). In these streams there is an invertebrate community adapted to breaking down the organic materials (Vannote *et al.* 1980). The partially consumed organic materials and the invertebrate production they sustain are carried downstream where they sustain communities of larger organisms. This longitudinal ecological gradient, described as the "River Continuum Concept" (Vannote *et al.* 1980; Minshall *et al.* 1985), extends all the way from the headwater streams to the river's mouth.

Coarse woody debris are the second major organic input from the riparian zone. The importance of the debris, mainly tree trunks and other large pieces of wood, is primarily structural. In small streams coarse woody debris assists in the development of a distinct pool and riffle morphology where fast shallow reaches alternate with slow deep pools (Keller and Swanson 1979; Frissell *et al.* 1986; Grant *et al.* 1990). By slowing and redirecting water movement, these structures can significantly slow the movement of materials downstream (Heede 1972; Marston 1982; Naiman and Décamps 1997). This structural complexity in the stream channel is a very important feature of good fish habitat (Beschta and Platts 1986).

Biodiversity

Riparian zones, though a relatively small proportion of the landscape, frequently support the highest species richness and diversity (Gregory *et al.* 1991). Flooding and other recurrent disturbances within the riparian zone create a complex array of habitats varying in the intensity and frequency of disturbance, and in the amount and type of sediment and litter deposition. There are often areas free of vegetation cover that become available for plant colonization following floods. This habitat diversity allows numerous species with differing habitat requirements and regeneration niches to coexist (Naiman and Décamps 1997). The riparian zone frequently supports small populations of upland species (Naiman *et al.* 1993), and thus may be a refuge for those species from disturbances affecting the uplands. For example, it is thought that many tropical mesic species survived the Pleistocene droughts in riparian zones and later re-expanded to their former ranges (Meave and Kellman 1994). Riparian zones are prime areas for biodiversity conservation because they support a large proportion of the species found in a region in a relatively small proportion of the total landmass (Naiman *et al.* 1993).

Erosion Protection

Erosion in a streambed occurs when the stream power exceeds a critical threshold where the power becomes sufficient to transport a sediment load (Bull 1979). Vegetation in both the active channel and in flooded riparian areas increases that critical threshold of stream power because plant stems and leaves increase the roughness of the stream bed, slowing water flows, and the networks of roots stabilize the soils (Smith 1976; Bull 1979; Hickin 1984; Beschta and Platts 1986). The importance of riparian zone plants with extensive root and rhizome systems for preventing soil erosion is recognized in riparian zone management (e.g. Mallik and Rasid 1993; Mallik *et al.* 2001).

Landscape Corridors

The physical presence of numerous riparian corridors across the landscape may be another important ecological service provided by riparian zones (Naiman and Décamps 1997). Some researchers have considered the importance that these corridors have for the movements of terrestrial animals (e.g. Merriam 1991; Machtans *et al.* 1996), however the subject has not been extensively studied (Naiman and Décamps 1997). There may also be detrimental aspects to landscape corridors, for example, some exotic plants appear to spread through the landscape along riparian zones (DeFerrari and Naiman 1994). If the corridor function is important it is likely to become increasingly so as human activity increases the fragmentation of the natural landscape.

Riparian Vegetation Patterns

Riparian vegetation patterns are dominated by two major gradients. The longitudinal gradient extends along the length of the stream, while the lateral gradient extends perpendicular to the stream from the banks into the upland vegetation (Malanson 1993; Bendix 1994b). These gradients are determined by a number of environmental factors, primarily related to steam flow and flooding regime. The riparian zone vegetation at any point can be considered to be a unique combination of the longitudinal and lateral gradients and their associated environmental factors (Bendix 1994b).

Longitudinal Gradient

The longitudinal gradient is characterized by changes in vegetation determined by factors such as the distribution of fluvial landforms, variations in current velocity, and changes in the underlying geomorphology along the length of a stream. The distribution of fluvial landforms, such as the channel bed, point bars, and terraces, and the distinctive vegetation associated with each varies with watershed size and stream discharge (e.g. Hupp and Osterkamp 1985; Hupp 1986). Variations in current velocity and wave exposure can be important in determining the distribution patterns of the riparian vegetation (e.g. Nilsson and Holmström 1985; Nilsson 1987; Bendix 1994a; 1999; Roberts and Ludwig 1991). Riparian landform and vegetation patterns along the longitudinal gradient tend to be obscured by local variation due to the large scales over which the patterns occur. As a result, these patterns have received relatively little study.

Lateral Gradient

The lateral gradient of vegetation change, stretching from the streambank to the boundary with the upland vegetation, is a prominent feature of every riparian zone. The textbook picture of the lateral gradient is found in the riparian zones of larger streams in the temperate or boreal regions where a number of distinct vegetation zones are evident (Figure 1). The lowest zone is composed of submerged and floating aquatics within the continually inundated channel. The second zone, frequently found on newly emerged point bars, is composed of herbaceous plants, primarily grasses and sedges. These plants emerge from the shallow water and extend for a short distance onto the shore where they merge with the third level, typically composed of other species of annual and perennial grasses and herbaceous plants. Among the smaller plants, seedlings and small individuals of a range of pioneer shrub and tree species such as willows and cottonwoods can often be found. Above the herbaceous plant zones is generally a well-developed forest, first with a canopy composed of the pioneer species and later with various stages leading toward the local late-successional vegetation. All of the later zones include, as subordinate members, many of the species and life-forms that were dominant at the lower levels. Numerous studies have described these patterns in the riparian zones of many

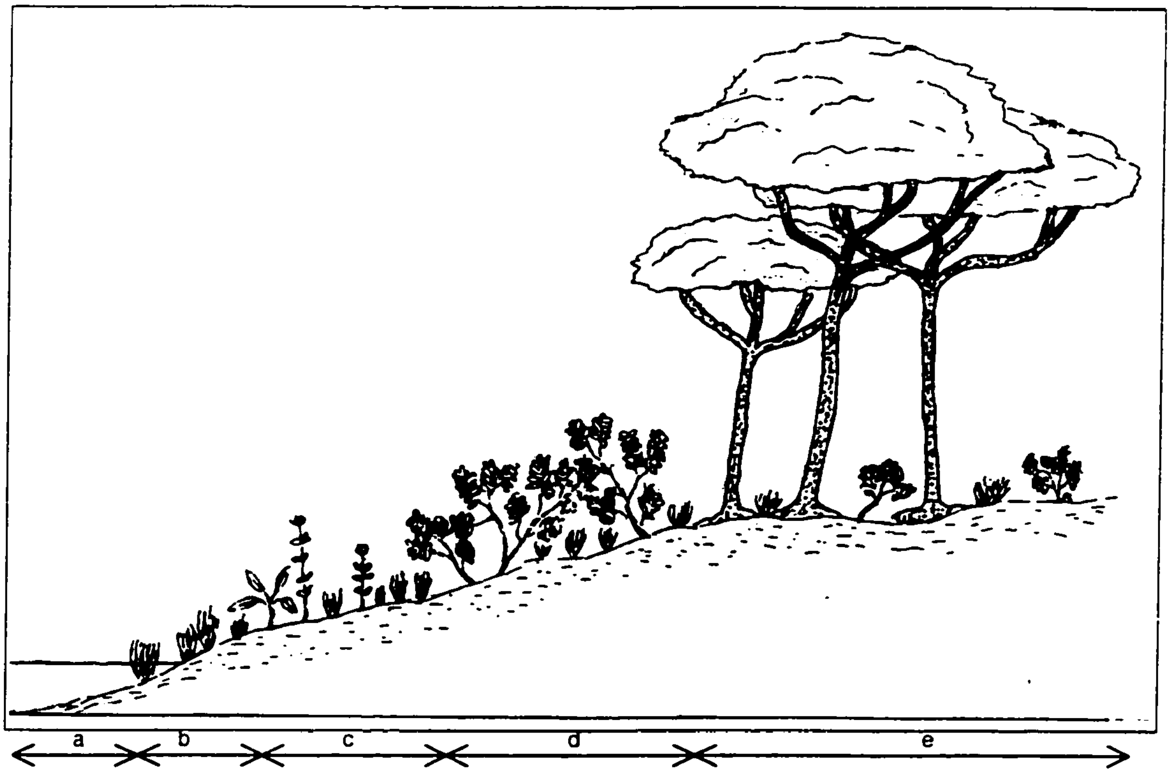

Figure 1: Vegetation zonation at a typical temperate region riparian zone divided into the a) submerged and floating aquatic, b) emergent aquatic, c) herbaceous, d) shrub, and e) forest sections. After Hupp (1983).

streams (e.g. Hefley 1937; Wistendahl 1958; Lindsey *et al.* 1961; Gill 1973; Hupp 1983; Farjon and Boagers 1985; Osterkamp and Hupp 1984; Menges 1986; van Coller *et al.* 2000). Differences in the tolerance of species to environmental factors such as flooding is of paramount importance in producing this pattern, but there is also a successional component. The successional element is most evident in regions where erodeable substrates leave the stream free to meander across the riparian zone. At those sites, an orderly sequence of successional stages from the initial herbaceous community on newly-deposited point bars to very old forest on older depositional surfaces has often been documented (e.g. Bliss and Cantlon 1957; Nanson and Beach 1977; Salo *et al.* 1986; Walker *et al.* 1986).

The environmental factors that influence the patterns found along the lateral gradient are primarily related to flooding. Flooding frequency and the tolerance of plants to flooded conditions is frequently cited as the major cause of vegetation zonation along the gradient (e.g. Illichevsky 1933; Wistendahl 1958; Lindsey *et al.* 1961; Bell and del

Moral 1977; Hupp 1983; Menges 1986; Harris 1987; Streng *et al.* 1989; Blom *et al.* 1990; Van Splunder *et al.* 1995; Bornette and Amoros 1996). In addition, some studies have identified specific aspects of the flood regime that are important. For example, Robertson *et al.* (1978) identified the duration and depth of flooding as a major factor in species distribution, and Toner and Keddy (1997) found that the timing of flooding and the occurrence of a second flood to be important. Physical resistance to damage from water flows and the impacts of water-borne debris has been found to influence the distribution of some species (e.g. Lindsey *et al.* 1961; Sigafoos 1964; Frye and Quinn 1979; Streng *et al.* 1989; Hupp and Osterkamp 1996). Mortality from deposition of flood-borne sediment can be important (Nanson and Beach 1977; Douglas 1987). Other environmental factors, ranging from soil nutrients to herbivory, have also been observed to influence the distribution of riparian species, but the consensus in the literature is that flooding and flooding-related factors are the most important.

Small Stream Riparian Zones

The preceding discussion of riparian zone ecology is largely based on research carried out on medium to large streams. Much less is known about the patterns found in the riparian zones of very small streams (Hupp 1986). In many cases the riparian vegetation is only a very narrow strip embedded in the surrounding forest (Hupp 1986; Naiman *et al.* 1993). It is well known that the channel morphology of small streams is distinct, for example the "pool and riffle" structure, or an alternating series of deep pools and fast flowing shallows (Beschta and Platts 1986; Frissell *et al.* 1986; Grant *et al.* 1990). Small streams tend to be missing channel features such as the floodplain bottoms and channel shelves common on larger streams (Hupp and Osterkamp 1985; Beschta and Platts 1986; Hupp 1986). The lack of certain channel features results in a simpler vegetation structure, as much of the complexity in riparian vegetation arises from the distinctive vegetation found on each channel feature. In addition, many small streams in northwestern Ontario tend to be on bedrock substrates, preventing stream meandering and the development of the successional patterns frequently found along larger lowland streams. All of these factors tend to produce riparian zones with much less internal heterogeneity along the lateral gradient than is found along larger streams.

A final issue in small streams, especially those in the boreal forest is the influence of Beavers (*Castor canadensis*). Beavers primarily select second through fifth order streams to build dams, and, if their populations are not kept low by trapping, they may strongly influence 20-40% of the length of the streams (Naiman *et al.* 1986; Naiman *et al.* 1988). Beaver dams alter the hydrology and sedimentation patterns in the streams, which in turn can alter nutrient cycling and other processes in the riparian zone (Naiman *et al.* 1988). Sediment filled abandoned ponds frequently develop into the wet grass and sedge meadows found along these streams (Ives 1942; Naiman *et al.* 1988), and beaver foraging can have a strong impact on the composition of the woody vegetation surrounding a beaver pond (Naiman *et al.* 1988; Barnes and Mallik 2001).

Plant Strategies

The steep environmental gradients, and especially flooding have a profound influence on the plant communities of the riparian zone. To meet these challenges riparian plants employ a variety of life-history, morphological, and physiological strategies. It is difficult to specify general riparian plant strategies because riparian zones are so variable worldwide, but there are some patterns. Adaptations to flooding, in contrast, appear to be more straightforward.

Riparian plant strategies vary with position along the lateral gradient. Co-ordination of the timing of vegetative growth and sexual reproduction with the flood regime is a common strategy used by plants to avoid the adverse effects of flooding (Blom *et al.* 1990; Blom *et al.* 1994; Blom and Voesenek 1996). Close to the stream, ruderal species are common, typically small annual plants that re-seed the floodplains every year (Lindsey *et al.* 1961; Menges and Waller 1983; van der Sman *et al.* 1993). Stress tolerant strategies are also used by some species, for example, *Rumex maritimus*, which adopts a strategy of "maintenance" during floods. These species concentrate on vegetative growth and damage prevention during flood years, and only put a great deal of energy into flowering in drier years (Blom *et al.* 1990). Further from the stream along the lateral gradient, the frequency and severity of flooding declines. Under these conditions species using a competitive strategy, including clonal species specialized for dominance in a high-light, low-disturbance habitat, can be found (Menges and Waller 1983). Close to the transition with the upland vegetation, species can be found with stress tolerant strategies equipped for the low light conditions of the forest understory (e.g. Bierzychudek 1982).

Morphological and physiological adaptations for survival under flooded conditions are important in many riparian plants (Kozlowski 1984; Blom and Voesenek 1996). Flood injury to plants typically occurs through one of two primary mechanisms, either from waterlogging of the soil and the creation of an anaerobic soil environment, or from physical damage caused directly by inundation and impacts of flood-borne debris. Waterlogging occurs when water fills the pore spaces in the soil, preventing the diffusion of gasses. The metabolism of root tissue and soil organisms causes oxygen levels to fall and gasses such as CO_2 to build up until the soil becomes almost entirely anaerobic (Ponnamperuma 1984; Blom and Voesenek 1996). The anaerobic environment affects metabolically active plants most strongly; many species avoid these effects by remaining dormant through the flooded season (e.g. Hall and Smith 1955; Kozlowski 1984). Species that are metabolically active under anaerobic conditions typically have relatively long root systems with large numbers of lateral roots concentrated near the soil surface and aerenchyma, cortical tissue that contains numerous intercellular spaces. These adaptations both increase the probability that some roots of the plant will not be in anaerobic soil and enhance the diffusion of oxygen throughout the root system. Many flood tolerant species also have a rapid growth response mechanism in the stems and petioles, mediated by ethylene and other hormones to respond to complete submergence. This "flood response" helps the plant to rapidly raise the shoot tip above the floodwaters (Blom *et al.* 1990; Blom *et al.* 1994). Physical damage from floodwaters can occur when a plant is struck by flood-borne debris or the roots are undermined by erosion (e.g. Ware and Penfound 1949; Sigafoos 1964). Species with flexible stems and strong anchoring root systems can have an advantage in these conditions. Graminoids, for example, have compact and flexible stems with the meristem protected at the base of shoot that are resistant to physical damage from flowing water (Menges and Waller 1983; Roberts and Ludwig 1991).

Riparian Management

Riparian management is a major concern in every landscape where human activity encroaches on streams. Forestry operations can disrupt the ecological services provided by the riparian zone resulting in deterioration of stream water quality and disruption of fish populations (Binkley and Brown 1993; Naiman and Décamps 1997). As a result, riparian and stream management practices in a forested landscape are directed toward maintaining the provision of the five ecological services. In some cases expensive remediation programs have been carried out to restore ecological services once provided by the riparian zone (e.g. Petersen *et al.* 1992), but preventative strategies that maintain healthy riparian vegetation are clearly preferred. The most effective riparian management practices typically involve the use of some form of buffer zone or riparian reserve between the stream and the land use in question. As a result, buffer zones have become enshrined in many management recommendations and government regulations (e.g. Lynch *et al.* 1985; Cohen *et al.* 1987; Ontario Ministry of Natural Resources 1988; Phillips *et al.* 2000).

There has been a wide array of research carried out on riparian buffer zones and their effectiveness in protecting stream water quality (for reviews see Clinnick 1985; Pike and Racey 1989; Norris 1993; Castelle *et al.* 1994). It has been demonstrated that riparian buffer zones are capable of reducing nutrient concentrations in surface runoff and shallow groundwater flows before the water enters the stream (e.g. Karr and Schlosser 1978; Martin and Pierce 1980; Peterjohn and Correll 1984; Norris 1993; Osborne and Kovacic 1993). This short-term filtering effect is important, though the role of the riparian vegetation as a long-term nutrient sink is unclear. For example, Osborne and Kovacic (1993) observed that during the dormant season riparian buffer vegetation released some of the nutrients back to the stream water. Nutrient flushes entering streams are a concern following forestry operations, but the most important impact on stream water quality that clearcutting and forestry road building have are sediment inputs (Binkley and Brown

1993). A number of studies have demonstrated that buffer zones can be effective in preventing sediment movements from clearcuts and forestry roads into streams (e.g. Trimble and Sartz 1957; Karr and Schlosser 1978; Lynch *et al.* 1985; Norris 1993). The overall importance of these buffers in maintaining stream water quality, however, is not entirely clear, as it has been demonstrated that road crossings, rather than clearcuts, are the most important source of sediments in many streams (e.g. Grayson *et al.* 1993; Kreutsweiser and Capell 2001). It has also been demonstrated that buffer zones can be effective in preventing increased stream water temperatures following clearcutting (e.g. Brown and Krygier 1970; Binkley and Brown 1993; Brosofske *et al.* 1997).

The minimum width necessary for a riparian buffer to be effective is a major question in the buffer zone literature. Thirty meter buffers are commonly recommended (Clinnick 1985; Castelle *et al.* 1994), though in some situations, for example on steep terrain or some agricultural settings, buffers of 90m or even 200m may be necessary (e.g. Ontario Ministry of Natural Resources 1988; Castelle *et al.* 1994). New research continues to re-evaluate these recommendations, for example a recent study in Washington state suggested that the widths recommended in many regulations may be inadequate to prevent changes in the riparian microclimate (Brosofske *et al.* 1997). More study is clearly warranted, especially given the economic pressures to release the land held inside buffers for timber harvest and agricultural use.

A second issue, equally as important as buffer width, is the minimum size of stream that should be protected with a buffer zone. Small streams make up a substantial proportion of the stream length in a landscape, for example, in an average fifth order watershed 90 percent of the stream length is made up of small streams of the first through third orders (Beschta and Platts 1986; Meyer and Wallace 2001). Yet, management regulations are typically aimed at medium and larger sized streams (e.g. Beschta and Platts 1986; Ontario Ministry of Natural Resources 1988; Meyer and Wallace 2001). A buffer zone is only effective for filtering pollutants from water entering the stream through shallow overland flow or surface runoff, as once the water becomes channelized it cannot be effectively filtered (Norris 1993). In a watershed where the smallest streams are not protected this means that a substantial portion of the flow volume in a particular stream will not have been filtered. In addition, the headwater streams have great value for biodiversity protection. The riparian zones of these small streams form extensive networks through every part of the landscape, that may be important for maintaining habitat connectivity and managing other conservation concerns at the landscape level (Naiman *et al.* 1993). In addition the aquatic communities of these small streams often have an invertebrate community unique from those of larger streams and often support very rare species (Meyer and Wallace 2001). Whether or nor these small headwater streams should be included in a management plan is a major concern. Objective, evidence-based rationale for inclusion or exclusion of these streams must be clearly articulated.

Study Area

The study area is located in the boreal mixedwood forest northeast of Thu Bay, Ontario, Canada (Figure 2). Undisturbed and buffer zone sites were located tributary streams to the Mackenzie, Spruce, and Wolf rivers, all of which drain to Superior. Burn sites were located in the 1999 Nipigon burn on streams tributary t

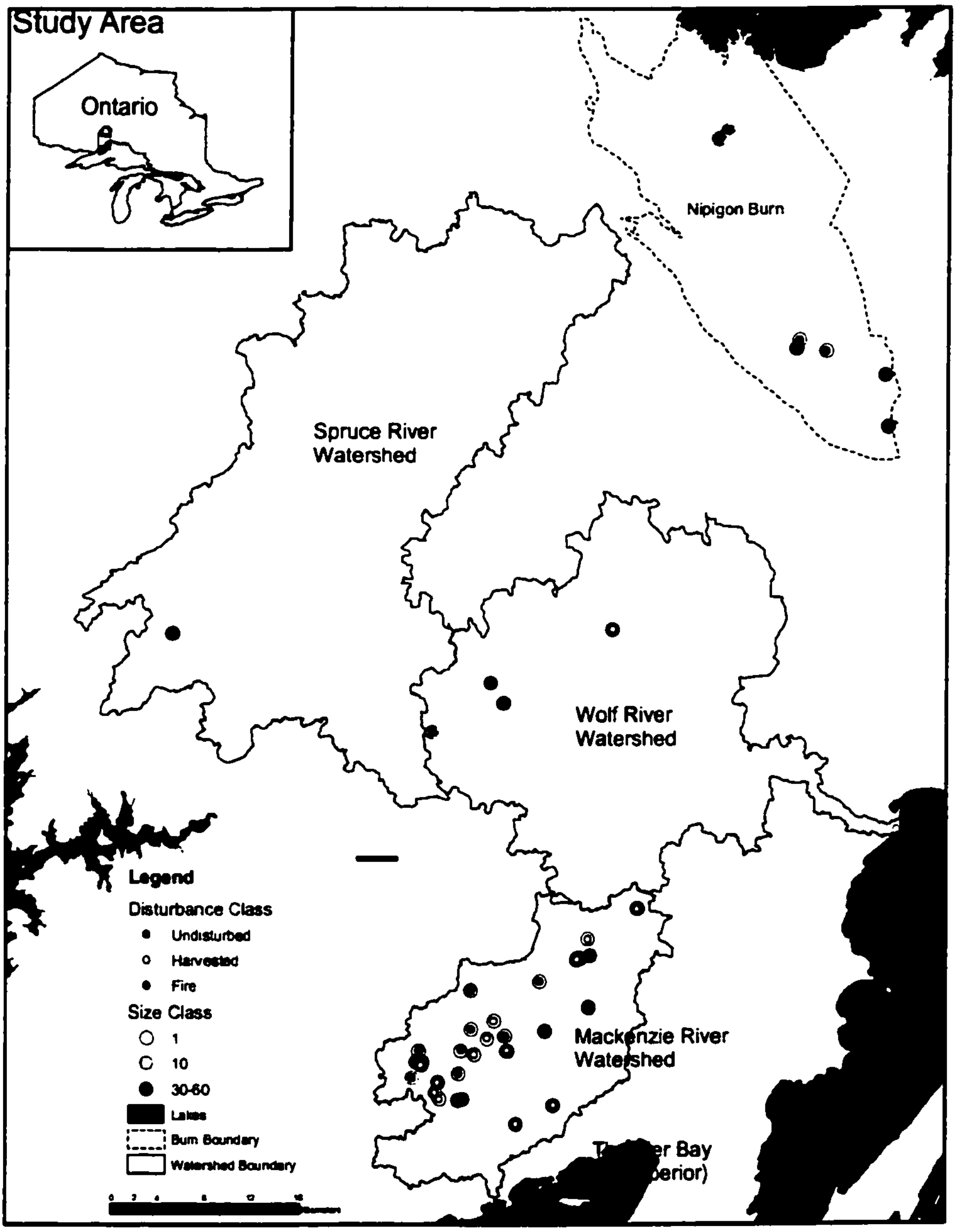

Figure 2: Map of the study area northeast of Thunder Bay, Ontario, Canada. The three study watersheds are outlined, as is the Nipigon burn.

Black Sturgeon River. The study area has low rolling relief with a bedrock substrate overlain by glacial tills. Temperatures vary widely from a mean daily minimum between -20°C and -26°C in January to a mean daily maximum between 22°C and 25°C in July. Mean annual precipitation ranges between 700mm and 850mm (Baldwin *et al.* 2000).

The riparian zone vegetation along these streams can be broadly separated into three types based on the local wetland ecosite classification guidelines (Harris *et al.* 1996; Rankin 2000): *Calamagrostis canadensis* and *Carex aquatilis* dominated meadow marshes, *Alnus incana* dominated swamp thickets, and occasionally a *Thuja occidentalis* dominated conifer swamp. The upland forests are a range of boreal mixed wood and conifer-dominated stands typical of the southern boreal forest (Rowe 1972). The upland forests are heavily impacted by forestry activity (Perera and Baldwin 2000).

The forty-two sites used in this study were identified and previously surveyed by the Comparative Aquatic Effects Program (CAEP) run by the Centre for Northern Forest Ecosystem Research (CNFER). This program identified potential sites using a GIS model of watershed areas and then determined the suitability of sites on the ground. The CAEP field crews later surveyed sites in detail. These surveys concentrated on the aquatic habitats including measurements of stream physical parameters and electrofishing surveys of the fish populations. See Appendix 1 for a complete list of the sites used in this study.

For the present study, sites were selected from three watershed size classes and three disturbance classes (Table 1). Watershed area was used instead of stream discharge *per se* because it is a practical and consistent method for selecting streams of varying size. Undisturbed sites were used for descriptive work and served as controls for

Table 1: Number of sites in each of the three watershed area classes and disturbance classes (Total = 42)

Disturbance Class	Watershed Area			Total
	100ha	1000ha	3000-6000ha	
Undisturbed	8	4	6	18
Cut with Buffer	7	6	4	17
Burn	2	5	-	7

comparisons between disturbance types. The sites assigned to each treatment group encompassed the full range of riparian vegetation found in the study area, from thicket swamp and meadow marshes ecosites to sites with very narrow conifer swamp riparian zones (Harris *et al.* 1996; Rankin 2000).

Sites were determined to be undisturbed if there was no adjacent forestry activity within 80-90m of the riparian-upland transition, as it is unlikely that serious edge effects would penetrate that far through the forest canopy with the strength to influence the riparian zone vegetation. In practice, this criteria meant that some sites with adjacent clearcutting with the mandated buffer width were classified as undisturbed. These unusual sites were typically found in deep valleys and had a narrow riparian zone, so the 90m buffer met the undisturbed criteria.

Buffer zone sites had an adjacent clearcut on at least one side of the stream that was separated from the stream by a buffer zone as recommended by the provincial guidelines (Ontario Ministry of Natural Resources 1988). The guidelines define an "area of concern" along coldwater streams ranging in width from 30m on slopes of less than 15% to 90m on slopes greater than 46%. These guidelines only designate an area of concern along streams large enough to show on a 1:50 000 map; unmapped streams are not planned for. This area is to be measured from the high water mark, but in practice it is defined as the beginning of woody vegetation, so many of these areas include both shrub-dominated riparian vegetation and a strip of upland forest. In the boreal region, this zone is normally left unharvested as a "riparian reserve". As a result, a typical stream is protected by the undisturbed riparian zone and an additional strip of upland forest. This strip of upland forest, which is variable in width, will be referred to as a "buffer zone" for the rest of this chapter. In most cases along the 1000ha and 3000-6000ha streams surveyed in this study, the buffer zone was the recommended 30m wide. Two sites, however, had cutting closer to the stream edge, and hence narrower buffers. The buffer zones of the 100ha streams were very variable in width, as not all of these streams were covered by the regulations. In all cases however, the 100ha buffer sites had at least several meters of upland forest buffer between the stream and the clearcut.

Burned sites were within the boundaries of the 1999 Nipigon-10 fire. At burned sites, the upland vegetation near the stream was almost entirely early-successional shrubs and herbs. The fire had consumed all but a small number of remnant trees up to the riparian-upland transition. Beyond some scorching and other damage to the upper branches of some *Alnus incana*, there was little fire damage evident in the riparian zone.

General Methods

This section describes in detail the field methodology used in this study and the statistical procedures used for data analysis. Summaries of the material in this section relevant to each chapter and details of the analyses carried out for specific objectives can be found in the methodology sections of individual chapters.

Field Sampling

At each site vegetation data were collected from four transects laid out across the riparian zone perpendicular to the stream (Figure 3). Two pairs of transects approximately 40m apart were placed on each side of the stream. On each transect one $1 m^2$ quadrat was placed at the edge of the stream, one was placed on the ecotone between the riparian zone and the upland vegetation, and up to three quadrats, depending on

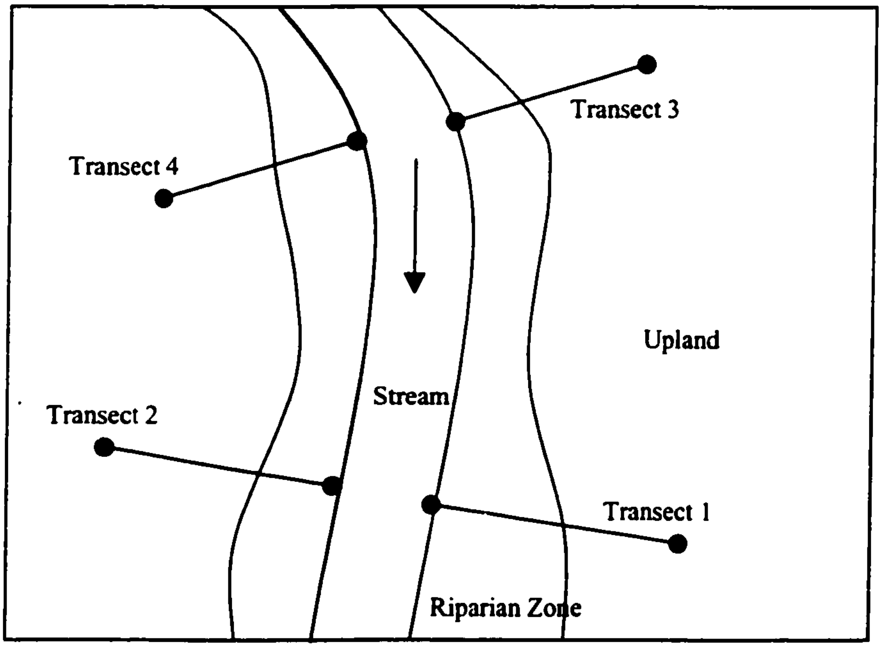

Figure 3: General schematic of the sampling regime at each site. The pairs of transects are spaced approxamately 40m apart along the length of the stream. Depending on site type, each transect would extend 20m to 30m into the upland.

riparian zone width, were spaced between the two across the riparian zone. The position of the riparian-upland ecotone was subjectively determined to be the location of the most rapid shift from predominantly riparian vegetation to upland vegetation. The distance of each quadrat from the stream and the width of the riparian zone along each transect were recorded. At transects across a riparian zone less than 1m wide only one quadrat was placed. Each transect was extended into the upland to collect understory vegetation data there. At undisturbed sites 3 upland quadrats spaced 10m apart were sampled on each transect. At buffer zone sites two upland quadrats were sampled per transect, either 10m apart, or if the buffer zone was narrower, closer together. Similarly, at burned sites two upland quadrats 10m apart were sampled on each transect. In each quadrat, the percent cover of all vascular and non-vascular plants was estimated by eye.

Most plants were identified to species, but some that are impractical to distinguish in the field without flowers or fruit, such as some grasses and sedges, were identified to genus. Specimens of each species were collected and identified later in the lab. Voucher specimens are deposited in the Claude Garton Herbarium (LKHD) at Lakehead University. Species that were lumped together during field sampling and for analysis are noted in Appendix 2. Several common and distinctive bryophytes were identified to species, the others were identified to genus or placed in general categories. Nomenclature follows Newmaster *et al.* (1998).

Statistical Analysis Techniques

Nonmetric-Multidimensional Scaling

Nonmetric-Multidimensional Scaling (NMS) is a non-parametric ordination method well suited to community data (Kenkel and Orlóci 1986; Clarke 1993). NMS uses the rank orders of samples in the distance matrix, hence it avoids the assumptions of multivariate normality made by traditional ordination methods, and regularly violated by most sets of community data (Williams 1983; Clarke 1993). In the first stage of an NMS analysis, the samples are arbitrarily placed in an n-dimensional space and their positions are refined using an iterative procedure. The goal is to move the samples into positions where the rank order of their distances is nearly the same as their respective rank orders from the distance matrix. The agreement between the two orders is measured by the stress value, with a stress of 0 indicating complete agreement. NMS is different from other ordination methods in that the number of dimensions (axes) that give the best solution must be chosen. In general, stresses are lowered in higher-dimensional solutions, but lower-dimensional solutions are more easily interpreted. The general method is to calculate solutions for a number of dimensions and to plot stress against dimensionality (scree plot). There is generally a point at which adding new dimensions gives only minor reductions in stress. Since the arbitrary starting conditions of any particular solution differ it is important to repeatedly run an NMS at each dimensionality. This ensures that the best solution found is likely not an artifact caused by the calculations becoming trapped in a local minima. The autopilot mode (slow and thorough option) in NMS in PC-ORD v.4 (McCune and Mefford 1999) calculates one through six dimensional solutions for 40 initial configurations. The best solutions for each number of dimensions are saved and the appropriate dimensionality selected. The data is then randomized and 50 additional solutions calculated to ensure that the best solution found for the raw data is better than random. The percent of variation in the distance matrix accounted for by each axis in the final solution can be calculated. The final solution can be displayed and used for hypothesis generation like the output from any other ordination technique.

Multiple-Response Permutation Procedure

The Multiple-Response Permutation Procedure (MRPP) (Zimmerman *et al.* 1985) is a non-parametric analogue of Discriminant Function Analysis (DFA) that supports a multivariate test of the null hypothesis of no difference between a-priori groups of samples. MRPP avoids many of the assumptions of DFA that make the latter test inappropriate for many types of ecological data (Williams 1983). The MRPP is carried out by calculating the statistic delta, or the linear combination for all groups of the average pairwise distances between each sample within a particular group. The observed delta is then compared to a null distribution of deltas for all possible permutations of samples into groups of the same size(s). A probability of a delta smaller than the observed is calculated from the position of the observed delta in the list of possible deltas.

As the number of possible permutations to be calculated is frequently very large, a test statistic T is calculated from a Pearson type III distribution to derive the probability. A third statistic A, or the chance corrected within group agreement calculated from the observed and expected deltas, is used to measure the homogeneity within groups. An $A=1$ indicates that all of the samples within each group are identical, while an $A=0$ indicates that within group heterogeneity is equal to that expected by chance. An $A<0$ indicates that the heterogeneity within groups is greater than that expected by chance.

Indicator Species Analysis

Indicator species analysis (Dufrêne and Legendre's 1997) is a non-parametric method for identifying species that are significantly more frequent and abundant in one or more *a priori* treatment groups. An indicator value is calculated by multiplying the relative abundance of each species in a particular group and the relative frequency of the species occurrence in the samples of that group. The significance of the indicator values are evaluated using a Monte Carlo procedure where samples are randomly reassigned to groups and indicator values recalculated. The number of randomized indicator values higher than the observed are used to calculate a probability value.

Principal Component Analysis

Principal Component Analysis (PCA) is an eigenanalysis-based ordination technique that has commonly been used in plant ecology. The mathematics of PCA are complex, but can be described as the reduction of the dimensionality of a complex data set by identifying successive orthogonal axes that explain the maximum amount of variation in the data (Gauch 1982). Each PCA axis is represented by an eigenvalue that measures the amount of variation in the data that is accounted for by that axis. For each axis, an eigenvector containing sample scores is also calculated that contains information on how strongly samples are associated with that axis. A "broken-stick" eigenvalue can also be calculated for each eigenvalue as a measure of statistical significance for that axis (Jackson 1993). PCA is generally not considered suitable for ecological data because such data are frequently non-linear (Gauch 1982; Minchin 1987). When beta-diversity is high along a long gradient, this tends to produce an "arch effect" where the gradient is curved and projected along more than one axis (Minchin 1987). In sets of environmental and trait data, there are typically relatively few zeros, thus shortening gradients, and the data are more likely to meet the assumptions of linear responses. PCA is a powerful technique when the assumptions are met, and has been advocated for use on trait data (Minchin 1987; Semenova and van der Maarel 2000).

Chapter 1: Riparian Zone Vegetation Patterns of Small Coldwater Streams in Northwestern Ontario

Introduction

Riparian zones are complex and dynamic environments found at the interface between aquatic and terrestrial communities (Gregory *et al.* 1991; Naiman and Décamps 1997). Riparian zones are important for the ecological functioning of the entire landscape due to the numerous ecological services (Ehrlich and Wilson 1991) that they provide. Among these services are the filtering and buffering of surface runoff and shallow ground water entering the stream and the addition of organic material to the stream (Gregory *et al.* 1991; Naiman and Décamps 1997). Riparian zones are also important in landscape-level issues of biodiversity conservation (Naiman *et al.* 1993). Land uses in forested regions such as road construction and clearcutting can have significant impacts on stream water quality, and riparian zones form an important buffer protecting the stream from these impacts (e.g. Binkley and Brown 1993; Norris 1993). As a result, management interest in riparian zones is high, and there is a need for much basic research on riparian zone ecology.

The complex interactions of multiple environmental and disturbance gradients within the riparian zone results in diverse and dynamic plant communities (Gregory *et al.* 1991; Naiman and Décamps 1997). The major gradients of vegetation change in riparian zones are oriented in two directions: the longitudinal, or along-stream gradient, and the lateral, or streambank to upland gradient (Bendix 1994b). The longitudinal gradient is characterized by large-scale changes in plant community type associated with changes in channel morphology and variations in current velocity and the flood regime (e.g. Hupp and Osterkamp 1985; Hupp 1986; Nilsson 1987; Bendix 1999). Longitudinal gradient patterns are often diffuse and can be obscured by large site to site variation (e.g. Nilsson *et al.* 1989). In contrast, the lateral gradient is typically very distinct. There are often several distinct vegetation zones along the lateral gradient associated with the decreasing frequency and intensity of flooding that occurs with increasing distance from the stream (e.g. Wistendahl 1958; Lindsey *et al.* 1961; Bell and del Moral 1977; Hupp 1983; Bendix 1999). The relative tolerance of species to flooding (Blom and Voesenek 1996), and successional processes (e.g. Nanson and Beach 1977; Salo *et al.* 1986) are very important in the development of the distinct lateral zonation. Due to frequent disturbances and the wide range of edaphic conditions, riparian zones generally support very high biodiversity, both of riparian specialist species and small populations of typically upland species (e.g. Nilsson *et al.* 1988; Baker 1990; Gregory *et al.* 1991; Meave and Kellman 1994; Spackman and Hughes 1995; Naiman and Décamps 1997).

Most of the riparian zone research has been carried out along mid-size streams and larger rivers. In contrast, the riparian zones of small headwater streams have received comparatively little attention (Hupp 1986). The channel morphology of small streams is distinct from the larger ones. Major fluvial geomorphic features, such as a broad flood plain, are typically absent, while other features become more important, especially pool and riffle structures (Lewin 1978; Osterkamp and Hupp 1984; Beschta and Platts 1986; Hupp 1986). The riparian vegetation along small streams tends to be less complex than that of larger streams; in many cases there is only a very narrow strip of riparian vegetation embedded in the surrounding forest (Hupp 1986; Naiman *et al.* 1993). These small streams are of great ecological importance, however, as organic inputs to the headwater streams are a critical energy source for the entire stream ecosystem from headwaters to mouth (Vannote *et al.* 1980; Minshall *et al.* 1985). The high density of headwater streams on the landscape makes them vulnerable to large-scale land uses, especially since many of the smallest streams are often excluded from protection (e.g. Beschta and Platts 1986; Ontario Ministry of Natural Resources 1988). The data gaps on these small streams mean that many riparian management programs proceed without baseline data for objective evaluation.

Just as the riparian zones of small streams have been poorly studied, the riparian zone vegetation of streams in the boreal forest region of North America has been poorly studied. There have been studies of the riparian zone along a mid-size river in the northwestern boreal forest (Nanson and Beach 1977), on some major subarctic rivers (e.g. Farjon and Bogaers 1985; Gould and Walker 1999), and on lakeside riparian areas in the eastern boreal forest (Denneler *et al.* 1999). In addition, much work has been done in Scandinavia (e.g. Nilsson 1987; Nilsson *et al.* 1988; Nilsson *et al.* 1989). Despite the intense forestry activity in the region (Perera and Baldwin 2000), and regulatory concern for stream and riparian protection (Ontario Ministry of Natural Resources 1988), very little basic research has been done on the plant communities found in the riparian zones along boreal streams.

This study is an examination of the riparian zone plant communities found along small coldwater streams in the boreal mixedwood forests of northwestern Ontario. The overall objective of this chapter is to describe these plant communities and to provide baseline data that can fill some of the gaps in basic information on species distribution and abundance in these habitats. This study has four specific objectives:

1) To document the vascular plant biodiversity of small-stream riparian zones.
2) To describe the patterns of riparian species distribution and abundance along the longitudinal gradient of increasing watershed size.
3) To describe the patterns of riparian species distribution along the lateral gradient of increasing distance from the streambank.
4) To identify a set of indicator species that can be used to locate the ecotone between the riparian zone vegetation and the upland forest.

Methods

Field Sampling

Vegetation data were collected from riparian zones along small coldwater streams in the boreal mixedwood forest northeast of Thunder Bay, Ontario, Canada. The study area has low rolling relief with a bedrock substrate overlain by glacial tills (Baldwin *et al.* 2000). The riparian zone vegetation can be broadly separated into three types based on the local wetland ecosite classification guidelines (Harris *et al.* 1996; Rankin 2000): *Calamagrostis canadensis* and *Carex aquatilis* dominated meadow marshes (Figure 4), *Alnus incana* dominated swamp thickets (Figure 5), and occasionally a *Thuja occidentalis* dominated conifer swamp. The upland forest vegetation is a range of mixedwood and coniferous stands typical of the southern boreal forest (Rowe 1972).

Thirty-five sites were sampled in three watershed area classes (100ha, 1000ha, 3000-6000ha). Eighteen undisturbed sites were sampled that had no forestry activity within 80-90m of the riparian-upland transition. Seventeen buffer zone sites that had adjacent clearcuts separated from the stream by a buffer zone as mandated by the Ontario provincial guidelines (Ontario Ministry of Natural Resources 1988) were also sampled. At each site vegetation data were collected from four transects laid out across the riparian zone perpendicular to the stream. Two pairs of transects approximately 40m apart were placed on each side of the stream. On each transect one $1m^2$ quadrat was placed at the edge of the stream, one was placed on the ecotone between the riparian zone and the upland vegetation, and up to three quadrats, depending on riparian zone width, were spaced between the two across the riparian zone. The position of the riparian-upland ecotone was subjectively determined to be the point of the most rapid shift from predominantly riparian vegetation to predominantly upland vegetation. The distance of each quadrat from the stream and the width of the riparian zone along each transect were recorded. At transects across a riparian zone less than 1m wide only one quadrat was placed. Each transect was extended into the upland to collect understory vegetation data. At undisturbed sites 3 upland quadrats spaced 10m apart were sampled on each transect. At buffer zone sites two upland quadrats were sampled per transect, either 10m apart, or if the buffer zone was narrower, closer together. In each quadrat, the percent cover of all vascular and non-vascular plants was estimated by eye.

Most plants were identified to species, but some that were impractical to distinguish in the field without flowers or fruit, for example some grasses and sedges, were identified to genus. Specimens of difficult or unusual species were collected and identified later in the lab. Voucher specimens are deposited in the Claude Garton Herbarium (LKHD) at Lakehead University. Species that were lumped together during field sampling and for analysis are noted in Appendix 2. Several common and distinctive bryophytes were identified to species, the others were identified to genus or placed in general categories. Nomenclature follows Newmaster *et al.* (1998).

Data Analysis

Preliminary observations in the field indicated that there were no major differences in riparian plant community composition between undisturbed sites and sites with adjacent forestry activity and a buffer zone. The lack of any significant difference in riparian plant community composition between undisturbed sites and sites with a buffer zone was confirmed using a Multiple Response Permutation Procedure (MRPP) (Table 2). MRPP is a non-parametric analogue of Discriminant Function Analysis (DFA) that supports a multivariate test of the null hypothesis of no difference between *a priori* groups of samples (Zimmerman *et al.* 1985). Since the buffer zone sites were not significantly different from the undisturbed ones, they were included in the analysis to increase the sample size. The implications that the lack of significant difference between the two groups of sites has for forest management practices will be explored further in Chapter 2.

The analysis of the patterns of species distribution along the longitudinal gradient of watershed area and the lateral gradient of distance from the stream required a range of analytical approaches. Site to site analyses of the overall vegetation structure and the longitudinal gradient of watershed area were carried out using average percent cover data for each site. Mean cover values for each species were calculated from all riparian quadrats, including quadrats at the riparian-upland ecotone, at a particular site. Analyses of the lateral gradient were carried out using individual quadrat data. All multivariate

Table 2: Results of the MRPP testing the null hypothesis of no significant difference in community composition between the undisturbed sites and sites with adjacent clearcutting with a buffer zone. Average distance is the mean Euclidean distance between each pairwise combination of quadrats from a particular microhabitat. N is the number of quadrats sampled in each microhabitat. The observed delta is calculated from the data while the expected delta is derived from a null distribution. T is the MRPP test statistic, and A is the chance corrected within-group agreement. The MRPP was highly non-significant (P=0.7123).

Microhabitat	Average Distance	N	MRPP Statistics
Undisturbed	39.7571	18	Observed Delta= 37.8158
Buffer Zone	35.7604	17	Expected Delta = 37.5888
			T= 0.6652
			A= -0.00603

tests were carried out using the PC-ORD ver.4 program (McCune and Mefford 1999), and univariate statistics using SPSS ver.9.0 (SPSS 1999).

Patterns along the longitudinal gradient were examined from two perspectives. First, the overall riparian zone vegetation structure and trends in the data were explored using Non-Metric Multidimensional Scaling (NMS) using the autopilot option with a slow and thorough analysis and the default settings. NMS is a non-parametric ordination method well suited to community data because it does not make the assumptions of multivariate normality required by other ordination techniques (Clarke 1993). Trends in the distribution and abundance of individual species associated with watershed size were evaluated using Indicator Species Analysis (Dufrêne and Legendre 1997). Indicator Species Analysis is a non-parametric method for identifying species that are significantly more frequent and abundant in one or more *a priori* groups. An indicator value is calculated from the relative abundance and relative frequency of a species in the samples belonging to a particular group. The significance of the indicator value in the group where a species has the maximum value is evaluated using a Monte Carlo simulation of 1000 runs where quadrats are randomly reassigned to groups and indicator values recalculated.

The lateral gradient was examined with univariate statistical methods. In an exploratory ordination of riparian zone quadrats, the species changes along the lateral gradient were masked by the site to site variation. It has been common practice to split northwestern Ontario riparian zone vegetation into wetland ecosite types (Harris *et al.* 1996) to reduce site-to-site variation (e.g. Rankin 2000). I did not follow this approach, however, because the classification places a continuum of sites into arbitrary classes. Nearly every site classified as one ecosite type included species or patches of vegetation typical of other ecosite types. I felt that this artificial separation of the site types would obscure the relationship between individual species and proximity to the stream.

The position of each quadrat within the riparian zone was expressed as a proportion of the distance across the riparian zone, with plots at the stream edge recorded as 0 and plots transitional to the upland vegetation recorded as 1. This allowed sites with variable riparian widths to be compared, as the spatial distance across the riparian zone varied widely (Rankin 2000). The cumulative change in environmental conditions from the stream bank to the upland transition were likely similar between sites, as flooding frequency and intensity will vary with elevation above the stream rather than with distance. This assumption of continuous change across the riparian zone may not be met at every site, but it allows broad patterns of species abundance and distribution to be drawn from the large dataset. Patterns of increasing or decreasing abundance relative to proximity to the stream were expected for most species. The species displaying these patterns of abundance were identified using non-parametric Kendall correlations between species abundance and relative distance to the stream. Quadrats from transects across riparian zones less than 1m wide were eliminated from these analyses because the single quadrat spanned the entire gradient and could not be objectively classed as either at the streambank or at the upland transition.

Practical identification of the riparian-zone upland ecotone requires knowledge of species that are significant indicators of the habitats on each side of the ecotone. Species useful for differentiating riparian zone and upland vegetation were identified using Indicator Species Analysis (Dufrêne and Legendre 1997). All riparian and upland quadrats were used in this analysis with the exception of the quadrat from each transect that was directly on the riparian-upland transition.

Results

Biodiversity

The riparian zone vegetation along small northwestern Ontario streams is highly diverse. In this study, 154 vascular plant species from 105 genera were found in the riparian zone (Appendix 2). This represents 14% of the species and 25% of the genera known to occur in the Thunder Bay District (Thunder Bay Field Naturalists 1998). In addition, 11 common bryophyte genera were observed. These species numbers should be considered an underestimate as many of the species are represented by a single collection; surveys of new sites in these watersheds would likely identify many more species. The species list would also be greatly expanded if the full diversity of the bryophytes were represented. Exceptionally diverse groups of species in the riparian zone included the genus *Carex* and the ferns and fern-allies. Several important genera, including *Salix* and *Amelanchier*, are underrepresented in the species list because in the field flowering individuals were rarely found, making positive identification of species difficult. Among the less common species, extensive populations of three species considered locally rare in the Thunder Bay District, *Brachyelytrum erectum, Carex crinita,* and *Lycopodium selago*, were found (Thunder Bay Field Naturalists 1998).

The riparian zone vegetation is dominated by a relatively small number of species (Table 3). The most abundant species include the shrubs *Alnus incana* and *Rubus pubescens*, the herbs *Thalictrum dasycarpum, Galium triflorum*, and species of *Viola*, the

Table 3: Common riparian zone species. Frequency is the number of riparian quadrats the species was observed in. Mean percent cover is calculated across all quadrats. Mean percent cover when present is the mean percent cover of each species only in the quadrats where they were observed. Species with a low overall mean % cover, but high % cover when present have a very patchy distribution.

Species	Frequency	Mean %	Mean % Cover When Present
Viola species	80.25	3.93	4.89
Alnus incana	70.70	24.95	35.28
Unidentified Bryophyte species	70.06	4.63	6.61
Thalictrum dasycarpum	62.42	6.61	10.59
Calamagrostis canadensis	59.87	6.32	10.55
Galium triflorum	56.37	1.64	2.90
Carex species Group #1	54.46	2.70	4.95
Rubus pubescens	50.64	2.43	4.80
Athyrium filix-femina	43.95	4.88	11.11
Mertensia paniculata	36.62	1.90	5.19
Rubus idaeus	32.80	2.45	7.46
Carex species Group #2	32.17	1.62	5.03
Mitella nuda	32.17	0.89	2.76
Carex aquatilis	29.30	7.10	24.22
Mnium species	27.71	1.63	5.89
Cornus stolonifera	26.43	2.73	10.33
Aster puniceus	25.16	0.71	2.84
Lycopus uniflorus	24.52	0.65	2.67
Carex deflexa	21.97	1.05	4.78
Climacium dendroides	21.66	0.76	3.49
Eupatorium maculatum	21.66	1.42	6.56
Prunus virginiana	21.66	2.73	12.62
Acer spicatum	20.38	3.14	15.43
Maianthemum canadense	20.06	0.53	2.65

grass *Calamagrostis canadensis*, and the sedge *Carex aquatilis*. Many of the less common species were widespread but only found in small numbers in a particular population, while the remainder were rarely encountered in widely scattered populations. There is a significant upland component to the species richness of the riparian zones. Many common upland herbs and shrubs are found in small populations on slightly raised or drier spots. Upland species that are especially common in the riparian zone include *Aster macrophyllus*, *Rubus idaeus*, and *Carex deflexa*. Even species that prefer dry habitats, such as lichens of the genus *Cladina* (reindeer lichens), can occasionally be found within the riparian zone.

Longitudinal Gradient

The riparian zone vegetation in northwestern Ontario is highly variable from site to site, but the variation is only weakly related to the longitudinal gradient in watershed size. Riparian zone width is highly variable within each watershed area class (Table 4), however the Kruskal-Wallis test demonstrates that there are no overall significant differences in riparian width between area classes (χ^2=3.461, p=0.177). The NMS identified a two-dimensional optimum solution with a final stress of 12.014 that accounted for the majority of the site to site variation in the data (Figure 6). The proportion of variation in the distance matrix accounted for by the ordination is 0.230 and 0.676 for the first and second axes respectively, for a cumulative r^2 of 0.906. The first axis separated sites with a high component of *Alnus incana* and some associated understory species from sites without a high abundance of *A. incana*. The second axis, which accounted for the majority of the variation in the data, separates meadow marsh sites from sites with high shrub and herb components. Increasing riparian zone width was correlated with axis 2 (tau=0.464). Species axis loadings and correlations are listed in Table 5. *Alnus incana* was the only species with a strong negative loading on the first axis and a neutral loading on the second. Similarly, *Calamagrostis canadensis* and *Carex aquatilis* both had very high loadings on the second axis.

Table 4: Mean width, standard deviation of width (SD Width), and minimum and maximum distances (m) from the streambank to riparian-upland ecotone for each watershed area class.

Watershed Area	Mean Width	SD Width	Min Width	Max Width
100ha	7.3	6.6	0.5	35
1000ha	13.6	17.3	0.5	78
3000-6000ha	6.4	7.6	0.5	27

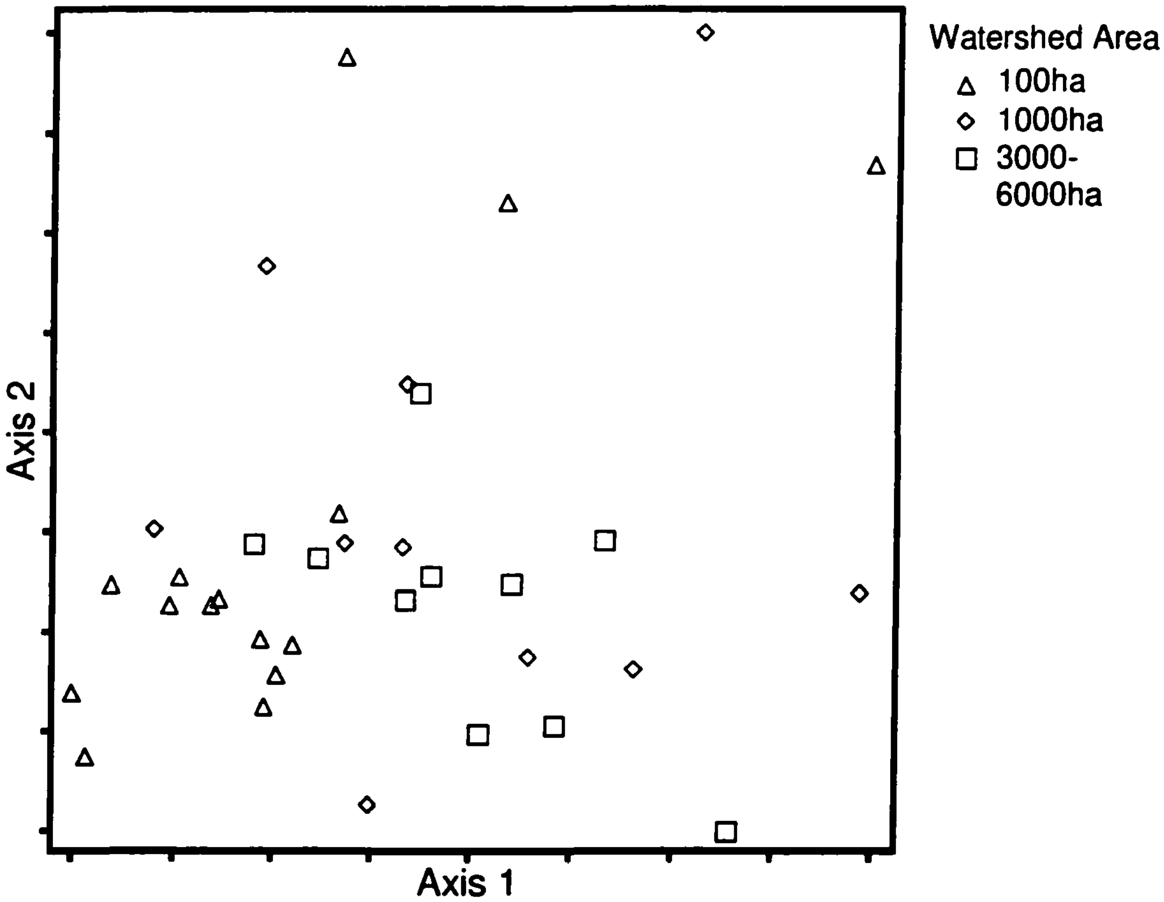

Figure 6: NMS of average site vegetation. Sites are divided into watershed area classes of 100ha, 1000ha, and 30-50km^2. Axis 1 separates sites with a high component of *Alnus incana* (the cluster of 100ha and 1000ha sites to the lower left of the figure) from sites without a high abundance of that species. Axis 2 separates sites with a high abundance of *Calamagrostis canadensis* and *Carex aquatilis* (the 100ha and 1000ha sites to the top of the figure) from sites without a high abundance of those species.

The weak association between the site to site variation accounted for in the NMS and the longitudinal gradient in watershed area is evident in the intermingled watershed area classes in Figure 6. The factor loadings in Table 5 indicate an association between *Alnus incana* and the cluster of 100ha and some 1000ha sites and a similar association between *Calamagrostis canadensis* and *Carex aquatilis* and the 100ha and 1000ha sites. These three species are characteristically found in high abundance at swamp thicket and meadow marsh sites respectively (Harris *et al.* 1996). This evidence suggests that these ecosite types are associated with the smaller 100ha and 1000ha watershed areas, and hence that the environmental conditions that promote the development of that vegetation type are also correlated with watershed.

Table 5: Axis loadings for each species and non-parametric Kendall correlations between the mean cover of each species at each site and site scores for the first and second NMS axes.

Species	Axis 1	Axis1 -tau	Axis 2	Axis 2-tau
Acer spicatum	-0.3106	-0.251	-0.7048	-0.508
Alnus incana	-0.2466	-0.603	-0.0907	0.062
Athyrium filix-femina	-0.2354	-0.329	-0.492	-0.559
Unidentified Bryophyte Species	0.0701	0.111	-0.3364	-0.458
Calamagrostis canadensis	0.3951	0.308	1.1619	0.610
Campanula aparinoides	0.1944	0.090	1.4854	0.444
Carex aquatilis	0.1192	0.253	1.2485	0.562
Carex rostrata	0.7899	0.324	1.7149	0.424
Chamaedaphne calculata	-0.0596	0.110	1.6292	0.473
Circaea alpina	-0.6027	-0.432	-0.5737	-0.179
Conocephalum conicum	0.3405	-0.002	-0.9599	-0.471
Corylus cornuta	0.0699	0.000	-0.5993	-0.508
Dicranum species	0.2601	0.251	0.7286	0.446
Dryopteris expansa	-0.2885	-0.437	-0.2326	-0.028
Ledum groenlandicum	-0.0760	0.026	1.4991	0.415
Matteuccia struthiopteris	-0.4930	-0.409	-0.6006	-0.253
Mitella nuda	-0.0229	-0.176	-0.5729	-0.600
Mnium species	-0.0877	-0.269	-0.5894	-0.525
Myrica gale	0.1359	0.246	1.2731	0.470
Scirpus cyperinus	0.9384	0.311	1.6491	0.421
Spiraea alba	0.0603	0.090	0.5917	0.512
Streptopus roseus	0.0336	-0.052	-0.5927	-0.441

Besides the weak association between wetland ecosite type and watershed area, some species also had distribution patterns related to the longitudinal gradient. Table 6 lists some common species, including *Circaea alpina*, *Eupatorium maculatum*, and *Aster umbellatus*, that were found by Indicator Species Analysis to be significantly more frequent and abundant in riparian zones of a particular watershed class. None of these indicator values are particularly high, however, reflecting the fact that all of these species were found, at least occasionally, at sites in all three of the watershed classes.

Table 6: Indicator values for some common species at each watershed class. Observed indicator values summarize the relative frequency and abundance of each species at the watershed class where they are most abundant. The mean randomized indicator values are calculated from 1000 Monte Carlo runs with randomized data. The p-value is the proportion of randomized runs that had indicator values higher than the observed.

Watershed Area	Species	Observed Indicator Value	Mean Randomized Indicator Value	p-value
100ha	*Circaea alpina*	48.0	22.6	0.015
	Dryopteris expansa	69.8	31.4	0.001
	Ribes hirtellum	40.8	25.8	0.048
1000ha	*Cirsium muticum*	44.6	27.5	0.032
	Pleurozium schreberi	51.5	30.7	0.038
	Solidago species	46.2	15.1	0.002
3000-6000ha	*Aster umbellatus*	48.0	28.0	0.018
	Climacium dendroides	66.5	41.5	0.020
	Diervilla lonicera	58.4	27.8	0.003
	Equisetum arvense	42.1	18.7	0.020
	Eupatorium maculatum	54.3	32.2	0.012
	Gentiana rubricaulis	40.0	12.3	0.010
	Pyrola species	30.0	11.9	0.041
	Sanicula marilandica	32.6	15.9	0.040
	Thalictrum dasycarpum	47.6	37.5	0.014

Lateral Gradient

Similar to the longitudinal gradient, the lateral gradient was diffuse, with the vegetation appearing homogenous across the riparian zone. The most striking feature distinguishing the riparian zone from the upland forest was the almost complete lack of canopy trees in the riparian zone. Large trees were occasionally found on drier patches within the riparian zone, but only scattered seedlings and saplings were common. The saplings were generally suppressed *Abies balsamea*. Overall, the riparian zone was dominated either by tall shrubs, primarily *Alnus incana*, or open meadows dominated by *Calamagrostis canadensis* and *Carex aquatilis*.

Though overall the riparian vegetation appeared homogenous across the lateral gradient, some species did have strong changes in abundance across the gradient. Species with significant correlations between abundance and relative distance from the streambank are listed in Table 7. Some species, including *Conocephalum conicum, Thalictrum dasycarpum, Eupatorium maculatum,* and *Cornus stolonifera,* were most abundant at the stream edge; those species decreased in abundance away from the stream. A second group of species, including *Cornus canadensis, Carex deflexa,* and *Aster macrophyllus,* increased in abundance away from the streambank toward the ecotone with the upland forest. The species that followed this pattern were all common upland species that were frequently found in small populations within the riparian zone.

Table 7: Kendall correlations between some important species and relative position in the riparian zone (n=418). Species with negative correlations are associated with the streambank, while those with positive ones are associated with the riparian-upland ecotone.

Species	tau	p-value
Aster macrophyllus	0.210	<0.001
Carex deflexa	0.217	<0.001
Climacium dendroides	-0.212	<0.001
Clintonia borealis	0.278	<0.001
Conocephalum conicum	-0.276	<0.001
Cornus canadensis	0.231	<0.001
Cornus stolonifera	-0.212	<0.001
Eupatorium maculatum	-0.242	<0.001
Thalictrum dasycarpum	-0.250	<0.001
Thallose Liverwort	0.268	<0.001

Riparian-Upland Ecotone

The vegetation change at the ecotone between the riparian zone and the upland vegetation was very abrupt and marked by a major change in understory species composition (Table 8). Species that were found by indicator species analysis to be significant indicators of the riparian zone include the shrub *Alnus incana*, the herbs *Thalictrum dasycarpum, Mertensia paniculata,* and *Viola* species, and the grass *Calamagrostis canadensis*. Species that were significant indicators of the upland vegetation include the herbs *Cornus canadensis*, *Maianthemum canadense*, and *Clintonia borealis*, and the bryophyte *Pleurozium schreberi*.

Table 8: Indicator values for some species useful for distinguishing the riparian zone from the upland. Observed indicator values summarize the relative frequency and abundance of each species in both the riparian zone and the uplands. Mean randomized indicator values are calculated from 1000 Monte Carlo runs with randomized data. The p-value is the proportion of randomized runs that had indicator values higher than the observed maximum indicator value.

Species	Riparian IV	Upland IV	Mean Randomized IV	p-value
Viola species	64	6	26.1	<0.001
Thalictrum dasycarpum	60	0	14.5	<0.001
Alnus incana	58	5	22.8	<0.001
Calamagrostis canadensis	57	1	18.5	<0.001
Galium triflorum	51	1	15.1	<0.001
Carex Species Group 1	48	1	15.6	<0.001
Athyrium filix-femina	36	2	12.9	<0.001
Rubus pubescens	34	9	19.8	<0.001
Mertensia paniculata	33	1	11.3	<0.001
Carex aquatilis	30	0	6.8	<0.001
Cornus canadensis	0	69	24.2	<0.001
Maianthemum canadense	3	55	25.5	<0.001
Pleurozium schreberi	0	50	17.5	<0.001
Clintonia borealis	2	48	22.6	<0.001
Vaccinium myrtilloides	0	41	15.0	<0.001
Dicranum species	0	38	14.1	<0.001
Abies balsamea	4	35	19.5	<0.001
Aralia nudicaulis	0	34	13.8	<0.001
Diervilla lonicera	0	33	13.8	<0.001
Trientalis borealis	3	33	17.3	<0.001
Linnaea borealis	0	31	11.4	<0.001

Discussion

Biodiversity

High vascular plant diversity is a common feature of riparian zones (e.g. Nilsson *et al.* 1988; Baker 1990; Gregory *et al.* 1991; Meave and Kellman 1994; Spackman and Hughes 1995; Naiman and Décamps 1997), and the riparian zones of northwestern Ontario are no exception. Most of the species are riparian specialists, but there is also a significant upland component to the diversity, as has been documented in other ecosystems (e.g. Meave and Kellman 1994). A major reason for the conservation value of riparian zones is the number of rare species that they can support (e.g. Nilsson *et al.* 1988). This study identified populations of three species rare in the region, and many more of the species found were only documented in single collections. This suggests that the true vascular plant diversity of these habitats is much higher, and thorough surveys of longer stream reaches would likely identify many more species. The riparian zone has been identified as a refuge from serious disturbances in the upland (Meave and Kellman 1994), though it is not clear in this ecosystem whether this is the case. Remnant and edge populations are important propagule sources for the recolonization by some forest specialist species into old fields (Matlack 1994a; Brunet and von Oheimb 1998), but this process has not been investigated in the boreal forest.

Longitudinal Gradient

There are striking differences in the riparian zone vegetation between sites, but these differences are only weakly associated with the longitudinal gradient of watershed area. The only large-scale pattern along the longitudinal gradient appears to be the watershed areas that the meadow marsh sites are found in. These sites were concentrated in the 100ha and 1000ha watershed size classes. These sites are likely abandoned and silted-in beaver ponds, indicating that the beavers are concentrating dam building on these smaller streams (Ives 1942; Naiman *et al.* 1988; Rankin 2000). This consistent with observations in central Ontario where the average watershed size of stream reaches with active or abandoned beaver dams was found to be between 500 and 1000ha, while reaches without dams had an average watershed size of more than 6000ha (Barnes and

Mallik 1997). Inconsistencies in the associations between ecosite and watershed area may be attributable to statistical artifacts from the relatively small sample size. It is more likely, however, that beaver habitat selection is based on many more factors than simple watershed size. Further research on the intricacies of beaver habitat selection will likely make these relationships clearer.

There were only very weak links between the distribution and abundance of individual species and the longitudinal gradient. Only fifteen of the 157 species found in the riparian zone were significantly associated with one of the watershed area classes (Table 6). The remainder of the species were either encountered too rarely for the patterns to be statistically significant, or they were relatively evenly distributed across all three watershed size classes. There are no clear explanations for the distribution of most of the species that do have a significant association, though some may be responding to differences in light levels. *Aster umbellatus* and *Eupatorium maculatum*, for example, are both large perennial herbs that are typically found directly at the stream edge in swamp thicket riparian zones. These species are likely responding to higher light levels along the streambank at the 3000-6000ha sites. The larger streams are often wide enough to be open to the sky, while along the smaller streams the stream is typically completely overhung with *Alnus incana*. Other abiotic factors associated with watershed area, such a change in the flood regime associated with larger watershed sizes (e.g. Rosentreter 1984) could also result in a similar distribution. It is, however, difficult to identify an environmental factor capable of producing such a pattern other than light that would also be consistent with the increase in abundance of these species observed following removal of the adjacent forest canopy along smaller streams (Chapter 2).

Lateral Gradient

The riparian zones of these small streams are internally quite homogenous, with the only distinct change at the riparian-upland ecotone. The distinct bands of vegetation common in the riparian zones of larger streams (e.g. Wistendahl 1958; Lindsey *et al.* 1961; Bell and del Moral 1977; Hupp 1983; Bendix 1999) are not found along these streams. Along larger streams the distinctive banding is caused by the complex fluvial geomorphology that occurs when a stream is on substrates that leave it free to produce a range of erosional and depositional features (Lewin 1978; Hupp 1986). The substrates of the streams in this study are frequently coarse glacial material or bedrock, which tends to constrain the streams, preventing the meandering patterns common in softer substrates, and producing the less complex riparian geomorphology. This lack of zonation could also be attributed to the relatively small scale of these riparian zones, as there may be little opportunity for a distinct zonation to arise when the major riparian species in many cases can form clones large enough to span much of the gradient. If this were the case, a more distinct zonation would be expected in the wider riparian zones, but such a pattern was not observed

The lack of canopy trees in the riparian zone is the most striking feature that distinguishes these riparian zones from the riparian zones of larger rivers. The higher terraces found in larger-stream riparian zones typically support extensive forests (e.g. Osterkamp and Hupp 1984). In the simpler riparian zones along these small streams, however, only seedlings and saplings of the canopy trees, especially *Abies balsamea*, are common. The presence of these small trees indicates that, though they can initially establish, there is some factor(s) preventing them from recruiting to the canopy. It is likely that flooding and waterlogged soils are the mechanism. The major canopy tree species in northwestern Ontario all have relatively low or no tolerance to anaerobic soils compared to the high tolerances of the major riparian species such as *Alnus incana* (Bell 1991; USDA, NRCS 2001). Even *Picea mariana*, a major boreal tree species that is commonly found in boggy areas, has a much lower tolerance than *A. incana*. The ability of the riparian species to remain metabolically active while flooded places those species at a competitive advantage over the conifers (Blom and Voesenek 1996). As has been observed along streams in other regions, the distinct shrub-tree transition at riparian-upland ecotone is likely at the limit of annual flooding (Hupp and Osterkamp 1985). Other competitive interactions with the riparian shrubs could also play a role in preventing the conifers seedlings from recruiting to the canopy. It is well known that certain upland shrub species in northwestern Ontario can suppress conifer growth through competition for light or rooting space (e.g. Mallik *et al.* 1997). If such a mechanism were operating we would expect succession to a conifer canopy would eventually occur, but in this region the shrub thickets appear to be stable, supporting the moisture hypothesis.

The species that do change in abundance across the lateral gradient are likely responding to small-scale gradients of light availability and flooding frequency. The species that are common at the streambank but steadily decline further within the riparian zone fall into two groups. In the first group are large herbs such as *Thalictrum dasycarpum* and *Eupatorium maculatum* and the shrub *Cornus stolonifera.* These species likely prefer the higher light levels found at the streambank. The second group includes two bryophyte species that appear to be specialized to microhabitats beside the stream channel. *Conocephalum conicum* was typically found on bare substrates at the edge of the active channel, while *Climacium dendroides* was common among the dense herb cover just above the active channel. The increasing presence of upland species closer to the riparian-upland ecotone is likely related to the decreasing influence of flooding. The extent of flooding by the spring freshet can be expected to vary from year to year, with the sections of the riparian zone furthest from the stream likely experiencing, on average, fewer floods of shorter duration than locations closer to the channel. During the growing season, flooding by summer storms may also be important. These storms can temporarily increase the flow rates in these streams, sometimes past the bankfull stage, causing short-term flooding of the sections of the riparian zone closest to the stream channel.

Riparian-Upland Ecotone

The ecotone between the riparian zone and the upland vegetation is the point of most abrupt change on the lateral gradient. As discussed above, the ecotone is likely maintained by flooding disturbance that prevents the establishment of canopy trees closer to the stream. The best practical indicators of the location of the ecotone, however, are understory species. The point of transition between the two vegetation types can be frequently located to less than 1m based on the shift in understory species composition. The list of indicator species in Table 8 provides a basis for decisions on the location of the ecotone. Experience and judgement are needed, however, and decisions should be based on several species if possible. Many of the indicator species are ecologically quite flexible and can often be found "out of place". *Alnus incana* provides a case in point. *A. incana* is the single most common and dominant species in the riparian zone, and an important differential species in the keys in the local ecosystem classification guide (Harris *et al.* 1996). Use of only this species to delineate the boundaries of a riparian zone, however, may lead to incorrect placement. In the present study, *A. incana* has been anecdotally observed to dominate in patches of upland adjacent to the riparian zone years after a windthrow event removed the canopy trees (Chapter 2). Inclusion of other species will help to correctly place the transition zone in otherwise ambiguous situations.

Chapter 2: The Impact of Adjacent Clearcutting and Forest Fire on Riparian Zone Vegetation in Northwestern Ontario

Introduction

Healthy riparian zone vegetation is an important component of any management plan for the maintenance of good stream water quality and fish habitat. Riparian zones form the interface between the terrestrial and aquatic ecosystems and provide a range of ecological services (Ehrlich and Wilson 1991) critical for maintaining ecological function within a stream (Gregory *et al.* 1991; Naiman and Décamps 1997). Riparian zones filter and buffer runoff, preventing sediments, pollutants, and excess nutrients from entering the stream (Norris 1993; Naiman and Décamps 1997). Riparian zones are also important sources of organic matter for the stream, as inputs of leaf litter and woody debris to headwater streams are a major source of energy, nutrients, and structural materials for the stream ecosystem (Vannote *et al.* 1980). In addition, corridors of riparian vegetation through the landscape have been advocated as a solution for managing regional biodiversity and maintaining ecosystem function (Naiman *et al.* 1993). The impact of natural and anthropogenic disturbances on the riparian plant community is of major concern, since this can disrupt or alter the provision of ecological services.

The type of land use occurring in the upland vegetation can influence the riparian zone plant community. For example, Stevens and Cummins (1999) found significant differences between riparian zones in woodlands and those beside agricultural and pasture land. In the boreal forests of northwestern Ontario the dominant land use is forestry (Perera and Baldwin 2000). The impact of streamside clearcutting on the riparian zone is a major concern, since many of these streams support important stocks of brook trout and other sport fish species. The negative impacts that forestry can have on stream water quality are well documented (e.g. Binkley and Brown 1993). There has been a great deal of research done demonstrating the effectiveness of such buffers in preventing excess sediment and nutrient inputs, ensuring sufficient coarse woody debris inputs to the stream, and avoiding increased stream water temperatures (e.g. Brown and Krygier 1970; Peterson *et al.* 1992; Norris 1993; Osborne and Kovacic 1993).

Buffer zones are an important component of the Ontario provincial guidelines for the protection of fish habitat (Ontario Ministry of Natural Resources 1988). The guidelines define an "area of concern" along coldwater streams ranging in width from 30m on slopes of less than 15% to 90m on slopes greater than 46%. These guidelines only designate an area of concern along streams large enough to show on a 1:50 000 map; unmapped streams are not planned for. This area is to be measured from the high water mark, but in practice it is defined as the beginning of woody vegetation, so many of these areas include both shrub-dominated riparian vegetation and a strip of upland forest. In the boreal region, this zone is normally left unharvested as a "riparian reserve". As a result, a typical stream is protected by the undisturbed riparian zone and an additional strip of upland forest. This strip of upland forest, which is variable in width, will be referred to as a "buffer zone" for the rest of this chapter.

In contrast to clearcutting, forest fires do not leave buffer zones along streams. Fires typically burn directly to the edge of the riparian zone and then either stop or jump the barrier. The predominantly broad-leaved riparian zone vegetation is less flammable and soil moisture levels are high so the vegetation is far less likely to ignite (Johnson 1992). High temperatures may damage the foliage and upper stems of some shrubs, but it is unlikely that the heat from a fire would be high enough to damage the root and rhizome systems. Some research has been conducted on the influence of fire on the canopy trees near streams (Russell and McBride 2001). However, very little research has been done on the response of the herbaceous and shrub components of riparian vegetation to an adjacent forest fire.

The buffer zones recommended by provincial regulations in Ontario (Ontario Ministry of Natural Resources 1988), encompass a large volume of wood, yet the role of forested buffers beyond the riparian zone in stream protection is unclear. Many small streams in northwestern Ontario have very wide riparian zones that likely provide all of the necessary ecological services to the stream. If there are no negative impacts on the riparian zone vegetation following removal of some of the adjacent canopy, then it may be possible to harvest some of this wood without negative impacts on the stream. In this chapter, I explore this possibility by comparing the responses of the riparian zone vegetation to adjacent clearcutting and fire to undisturbed sites. I expect that the response of a riparian zone plant community to an adjacent fire should be similar to clearcutting to the edge of the riparian zone. In both cases the main effects experienced by the riparian zone should be changes in environmental conditions caused by the removal of the adjacent canopy trees. The response of the riparian zone vegetation to clearcutting when protected by a buffer zone should be correspondingly less extreme. The objective of this study is to test whether there are any significant changes in the distribution and abundance of plant species in the riparian zone following fire and clearcutting with a buffer adjacent to the stream. The results of this study will assist in the ongoing evaluation of the current riparian management guidelines in Ontario.

Methodology

Study Sites

Vegetation data were collected at 42 sites in coldwater stream watersheds near Thunder Bay, Ontario. Sites from three watershed size classes (100ha, 1000ha, 3000-6000ha) and three disturbance classes (undisturbed, clearcut with a buffer, and forest fire) were sampled (Table 1). Sites were determined to be undisturbed if there was no adjacent forestry activity within 80-90m of the riparian-upland transition, as it is unlikely that serious edge effects would penetrate far enough through the forest canopy to influence the riparian zone. In practice, this criteria means that some sites with adjacent clearcutting with the mandated buffer width were classified as undisturbed. These sites were typically found in deep valleys and had a narrow riparian zone, so the 90m buffer met the undisturbed criteria. Buffer zone sites had an adjacent clearcut on at least one side of the stream that was separated from the stream by a buffer zone as recommended by the provincial guidelines (Ontario Ministry of Natural Resources 1988). In most cases along the 1000ha and 3000-6000ha streams surveyed in this study, the buffer zone was the recommended 30m wide. Two sites, however, had cutting closer to the stream edge, and hence narrower buffers. The buffer zones of the 100ha streams were more variable in width, as not all of these streams were covered by the regulations. In all cases however, the 100ha buffer sites had at least several meters of upland forest buffer between the stream and the clearcut. Burned sites were within the boundaries of the 1999 Nipigon burn. At burned sites, the upland vegetation near the stream was almost entirely early-successional shrubs and herbs. The fire had consumed all but a small number of remnant trees up to the riparian-upland transition. Beyond some scorching and other damage to the upper branches of some *Alnus incana*, there was little fire damage evident in the riparian zone. The sites assigned to each treatment group encompassed the full range of riparian vegetation found in the study area, from thicket swamp and meadow marshes ecosites to sites with very narrow conifer swamp riparian zones (Harris *et al.* 1996; Rankin 2000). Riparian plant communities frequently vary along a longitudinal gradient of watershed size (e.g. Hupp 1986; Bendix 1994b), however this is not the case along these northwestern Ontario streams. Between-site variation in riparian community composition is high, but very little of the variation is related to the longitudinal gradient of watershed size (Chapter 1). Due to the lack of a significant longitudinal gradient in the riparian vegetation, and because a sufficient sample of burned sites were not available in every watershed size class, all of these data were lumped together for analysis.

Field Sampling

At each site vegetation data were collected from four transects laid out across the riparian zone. Two transects approximately 40m apart were placed on each side of the stream. Along each transect one 1m^2 quadrat was placed at the edge of the stream, one was placed on the ecotone between the riparian zone and the upland vegetation, and up to three quadrats were sampled between the two across the riparian zone. At transects across a riparian zone less than 1m wide only one quadrat was placed. In each quadrat the percent cover of all vascular and non-vascular plants was estimated by eye. Most plants were identified to species, but some that are impractical to identify in the field without flowers or fruit, for example some grasses and sedges, were identified to genus. Samples of unknown plants were identified in the lab. Voucher specimens are deposited in the Claude Garton Herbarium (LKHD) at Lakehead University. Nomenclature follows

Newmaster *et al.* (1998). For a full species list and description of the riparian vegetation see Chapter 1.

Data Analysis

The average riparian zone widths from each site were compared were compared using a non-parametric Kruskal-Wallis test to confirm that there were no systematic differences between the three disturbance classes. The SPSS ver. 9.0 package (SPSS 1999) was used to carry out the test. The average percent cover of each species from all quadrats at a particular site, including the riparian-upland transition quadrats, was averaged giving a mean cover for each species at that site. The overall structure and trends in the data were explored using Non-Metric Multidimensional Scaling (NMS) using the autopilot option with a slow and thorough analysis and the default settings. NMS is a non-parametric ordination method well suited to community data that avoids the many of assumptions about the underlying structure of the data made by traditional ordination methods (Kenkel and Orlóci 1986; Clarke 1993). The hypothesis of no significant floristic differences between the three treatments was tested using a Multiple Response Permutation Procedure (MRPP) (Zimmerman *et al.* 1985). MRPP is a non-parametric analogue of Discriminant Function Analysis (DFA) that supports a multivariate test of the null hypothesis of no significant difference between *a priori* groups of samples. MRPP avoids many of the assumptions of DFA that make the latter test inappropriate for many types of ecological data (Williams 1983). Indicator Species Analysis (Dufrêne and Legendre1997) was used to identify species that were significantly more frequent and abundant at sites in one of the disturbance classes. The indicator values are calculated by multiplying the relative abundance of each species in a particular group by the relative frequency of the species' occurrence in that group. The significance of the indicator values are evaluated using a Monte Carlo simulation of 1000 runs where samples are randomly reassigned to groups and indicator values recalculated. All multivariate tests were carried out using the PC-ORD ver.4 program (McCune and Mefford 1999).

Results

The 42 sites examined contained a wide range of vegetation from meadow marshes to thicket swamps to very narrow riparian zones that is representative of the undisturbed riparian vegetation in northwestern Ontario (Rankin 2000; Chapter 1). Riparian zone widths were highly variable within and between sites, ranging from 0.5m to 78m, but the Kruskal-Wallis test confirms that there are no significant differences in mean riparian zone width between disturbance classes (χ^2=3.016, p=0.211). The NMS identified a 2-dimensional optimum solution (Figure 7). The solution is very strong as the correlations (r^2) between the distances in the final solution and the distances in the n-dimensional species space are 0.712 and 0.161 for the first and second axes respectively.

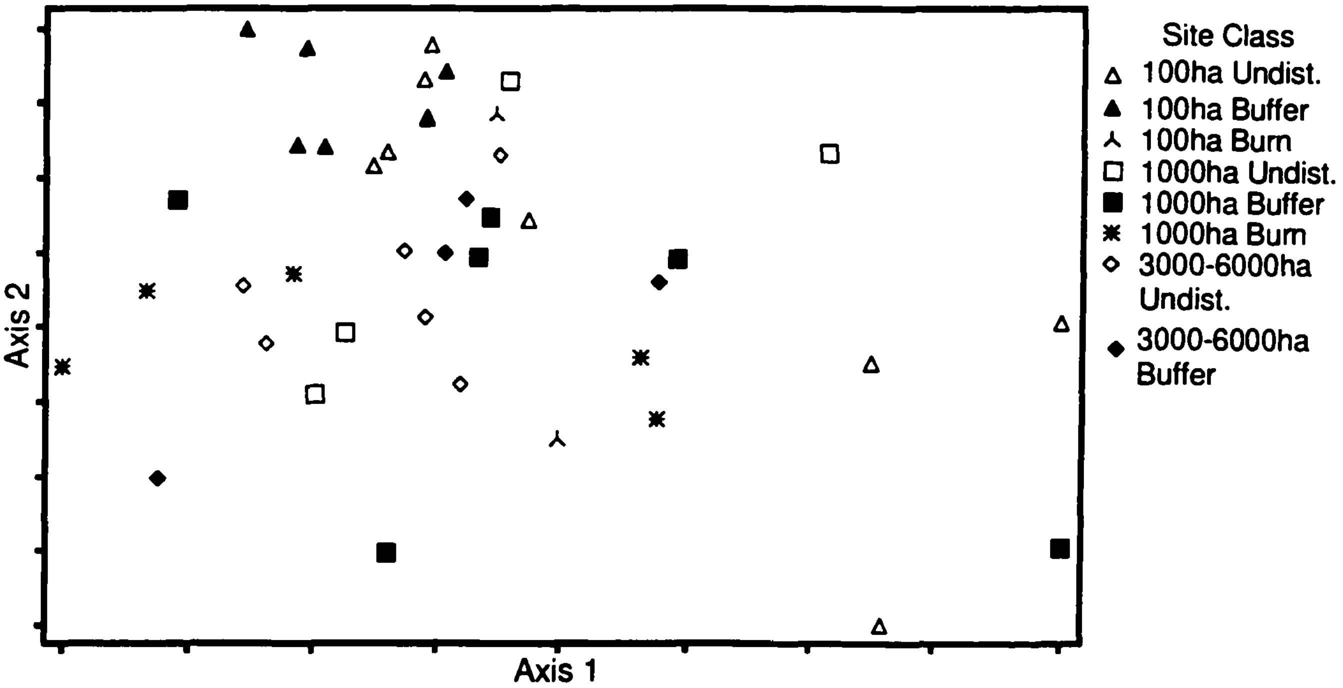

Figure 7: NMS ordination of average site data from all sites. The interspersion of all three disturbance types along gradients of riparian zone width and dominant species indicates that disturbance type does not have a systematic structuring effect on riparian zone composition. Axis 1 is a gradient from narrow riparian zones through shrub dominated ones to meadow marsh sites. Axis 2 is a gradient of increasing abundance of *A. incana*.

This gives a cumulative r^2 of 0.872, indicating that most of the variance structuring the dataset has been accounted for. Axis 1 represents a gradient from narrow riparian zones through riparian zones dominated by shrub thickets to open meadow marshes. Axis 2 appears to separate sites with high cover of *Alnus incana* and some associated herbaceous species from sites with a higher cover of other shrub and herb species. See Chapter 1 for a detailed discussion of the patterns of riparian species distribution found in northwestern Ontario. The three disturbance types are clearly interspersed in Figure 7. This suggests that any differences between the burned sites and the undisturbed and buffer sites are unlikely to be the result of spatial autocorrelation, even though the burn sites are spatially separated from the other treatments.

Any influence that disturbance may have on the riparian vegetation is clearly minor compared to the other factors structuring the vegetation. The MRPP (Table 9) demonstrates that there are no overall differences in riparian community composition associated with disturbance type. The MRPP is not significant and the low A-value indicates a great deal of heterogeneity within each disturbance class. The distance values indicate that the burn sites are the most different from the other two disturbance classes; this is supported by the much higher p-value (0.7123) found in an MRPP comparing only

Table 9: Results of the MRPP testing the null hypothesis of no significant difference in community composition between undisturbed sites, sites with adjacent clear-cutting with a buffer zone, and sites with an adjacent forest fire. Average distance is the mean Euclidean distance between each pairwise combination of quadrats from a particular microhabitat. N is the number of quadrats sampled in each microhabitat. The observed delta is calculated from the data while the expected delta is derived from a null distribution. T is the MRPP test statistic, and A is the chance corrected within-group agreement. The MRPP was non-significant (P=0.1850).

Microhabitat	Average Distance	N	MRPP Statistics
Undisturbed	39.7571	18	Observed Delta= 37.3359
Buffer Zone	35.7604	17	Expected Delta = 37.6671
Burn	34.936	7	T= -0.8083
			A= 0.0088

undisturbed and buffer sites (Chapter 1). These results are supported by the lack of any clear pattern related to disturbance type on scatterplot of sites in Figure 7. The major factor(s) structuring the riparian zone plant community in northwestern Ontario are clearly related to site to site variation, rather than disturbance type.

The Indicator Species Analysis demonstrates a slightly more complex story. Several species are significantly more frequent and abundant in the burned or buffered riparian zones (Table 10). Three of these plants (*Gymnocarpium dryopteris*, *Oryzopsis asperifolia*, and *Polytrichum* species) are upland plants common in northwestern Ontario, but rarely found in riparian zones. Their significantly greater occurrence at the riparian-upland ecotone at buffer zone sites likely has little biological significance. Two species, *Caltha palustris* and *Fraxinus nigra*, are important riparian zone species, are but are infrequently encountered in the study area (at 35% and 7% of sites respectively) and when found only in low abundance. Due to the relatively infrequent occurrence of these species, it is difficult to separate the possibility of a biologically significant response from statistical artifact. The remainder of the species display more interesting patterns. *Abies balsamea*, a shade tolerant conifer (Bell 1991), was significantly more frequent and abundant at the riparian-upland transition at buffer sites. Four other species (*Betula papyrifera*, *Populus tremuloides*, *Rubus idaeus*, and *Fragaria virginiana*) are much more abundant at the ecotone between the riparian zone and the upland at burned sites, and can often be found overhanging or extending into the riparian zone. These species are common early successional species in burns (Shafi and Yarranton 1973; Schaefer 1993). The remainder of the species (*Aster puniceus*, *Eupatorium maculatum*, *Galium triflorum*, *Lycopus uniflorus*, and *Scutellaria galericulata*) are widespread in northwestern Ontario riparian zones. These species increase strongly in abundance at the burn sites, especially those with narrow riparian zones.

Table 10: Indicator and randomized indicator values for species that are significant (p<0.10) indicators of one of the three disturbance classes.

Disturbance Type	Species	Indicator Value	Randomized Indicator Value	p-value
Undisturbed	*Polytrichum* species	44.2	29.2	0.044
Cut with Buffer	*Abies balsamea*	48.4	37.4	0.098
	Caltha palustris	42.0	23.9	0.037
	Gymnocarpium dryopteris	36.0	23.6	0.097
	Oryzopsis asperifolia	28.7	15.7	0.059
Burn	*Aster puniceus*	51.7	36.8	0.028
	Betula papyrifera	46.5	28.0	0.041
	Eupatorium maculatum	53.5	32.9	0.009
	Fragaria virginiana	57.7	25.5	0.004
	Fraxinus nigra	19.9	10.0	0.054
	Galium triflorum	43.8	37.7	0.050
	Lycopus uniflorus	66.8	38.8	0.001
	Populus tremuloides	40.8	12.5	0.004
	Rubus idaeus	51.4	41.0	0.066
	Scutellaria galericulata	57.4	28.4	0.009

Discussion

Vegetation Response

Our results indicate that, overall, riparian zones are not strongly affected by disturbances occurring in the upland vegetation. This makes sense in light of what is understood about the ecology of riparian zones. The primary factors that determine the distribution and abundance of riparian species are hydrologic. The lateral gradient of vegetation change in a riparian zone is determined by factors such as the frequency and intensity of flooding and the extent of saturated rooting zones (Bendix 1994b; Naiman and Décamps 1997). In northwestern Ontario the surficial geology (Rankin 2000) and beaver activity (Ives 1942; Naiman *et al.* 1988; Barnes and Mallik 2001; Chapter 1) are also important in structuring the riparian vegetation. Riparian species frequently have mechanisms such as tolerance for anoxic rooting zones that help them to survive flooding (Blom and Voesenek 1996). These species also frequently have dispersal and establishment strategies such as the ability to rapidly colonize bare sediments and aggressive clonal growth that allow rapid recovery from disturbance (Naiman and Décamps 1997). As long as a disturbance affecting the uplands does not significantly change the stream hydrology, there should be no major changes in the riparian zone vegetation.

The changes in the abundance of some common species are minor in relation to the overall stability of the vegetation. It is not surprising that the early-successional species such as *R. idaeus* and *P. tremuloides* that dominate the upland vegetation in the burn should also become more common at the riparian-upland transition. Similarly at buffer zone sites, the increase in abundance of *A. balsamea* near the riparian-upland transition may be due to increased light levels in the upland buffer due to edge effects from the nearby clear-cuts (Murcia 1995). The increase in abundance of riparian species such as *A. puniceus, E. maculatum, G. triflorum, L. uniflorus,* and *S. galericulata* is likely related to higher light levels in the riparian zone with the adjacent canopy removed. All four species are strongly rhizomatous and are capable of rapid clonal growth (USDA, NRCS 2001; Lamb *et al.* unpublished data). In undisturbed sites they are typically found in more exposed areas such as at the edge of the stream or as a component of meadow marsh vegetation. These species were abundant at burned sites with narrow riparian zones - the type of site where they are typically least abundant when the adjacent canopy is undisturbed. The increase in abundance of these large herbs is similar to that observed along Pennsylvania streams, where significant differences were found between riparian zones bordered by woodland and those bordered by agricultural and pasture fields (Stevens and Cummins 1999). It is unlikely, however, that these minor changes in the riparian plant community would alter the ecological services provided by the riparian zone in any major way.

I also have some anecdotal evidence that some riparian species may take advantage of a disturbance that disrupts the upland vegetation. I observed several cases of small-scale invasion by typically riparian species into upland patches near the riparian zone following windthrow and fire. Two common riparian species, *Alnus incana* and *Thalictrum dasycarpum*, were especially striking. *A. incana* frequently develops extensive thickets in old windthrow patches that bordered the riparian zone. These sites superficially resemble riparian thicket swamps, but the upland character of the understory species and the presence of large logs and stumps indicate the sites are not riparian. Scattered individuals of *T. dasycarpum* were found in recent cutblocks and burned areas as well as in small windthrow patches.

Alnus incana is a clonal species that can spread by layering and maintain dominance on a site by stem-base resprouting (Huenneke 1987; Bell 1991). *A. incana* does not spread rapidly, but established clones are very long-lived (Huenneke 1987). It is likely that, given the opportunity to establish in the windthrow gap, this species can dominate for a long period before conifers can displace it. *Thalictrum dasycarpum* appears to use a different strategy. *T. dasycarpum* is a wind dispersed species (van der Pijl 1969) with many ruderal characteristics (Grime 1979) that assists it in rapidly colonizing new sites. The species probably can establish rather quickly on the bare substrates available after a disturbance, but may soon be outcompeted by upland species. This behaviour is not surprising, as many riparian species are well known for their adaptations for the exploitation of small patches of bare soils scoured by floodwaters (Naiman and Décamps 1997). These observations indicate that, as a whole, the riparian zone plant community may have a comparatively stronger ability to disperse to and invade small patches than the upland community. This stronger colonization ability allows them to temporarily establish in sites outside of their normal environmental tolerances.

Management Implications

This study has significance for forest management practices, as it demonstrates that the buffer zones currently recommended by provincial regulations may need to be re-evaluated. Along streams where the riparian zone is extensive enough to supply all of the ecological services required, an additional buffer zone of upland vegetation might not always be necessary for effective stream protection. In these cases, partial harvesting in the buffer zone, or a reduction in the width of the buffer zone, is not likely to cause significant change in the riparian zone plant community. It is unlikely that there would be changes in the quality of the ecological services provided by the riparian zone if the vegetation is stable.

However, these suggestions need to be applied with great caution. Decisions regarding the buffer zone width should be made on a site by site basis depending on whether the riparian zone alone is capable of providing the necessary ecological services. At a site with a 30m to 50m wide meadow marsh or thicket swamp on each side of the stream it is unlikely that the adjacent upland vegetation is playing a significant role in maintaining stream water quality. A significant proportion of the streams in northwestern Ontario have riparian zones that are much narrower, however (Rankin 2000; Chapter 1). At these sites, the upland vegetation may be at least partially responsible for the provision of many ecological services. At sites with narrow riparian zones, a buffer of some form is likely necessary. When making these decisions, it must also be remembered that buffer zones function to protect other values besides stream water quality. For example, Whitaker and Montevecchi (1997) found that boreal riparian forests in Newfoundland support a distinctive bird community, including species found only in that habitat. Similarly, Machtans *et al.* (1996) found that lakeside buffer zones in Alberta provided important movement corridors for many bird species. These considerations must be taken into account in any management plan. We envision a flexible system where the buffer zone can vary depending on the width of the riparian zone, the physical characteristics of the individual site, and the non-stream values requiring protection.

For the sites with narrow riparian zones, further research on the role of upland buffers is needed. In particular, the width and characteristics of buffer zones of upland vegetation that will provide effective stream protection when the riparian zone is narrow need to be investigated. The influence of edge effects (Murcia 1995) on the long-term stability of the vegetation in a buffer zone is not well understood. It is well known, for example, that windthrow mortality along clearcut edges can be significant (Ruel 2000). Anecdotal observations of numerous windthrown trees at the sites in this study suggest that it may also be an important factor in riparian buffer zones in northwestern Ontario. Despite this, the details of edge effects are almost completely unknown in the boreal forest (Perera and Baldwin 2000). The lack of general knowledge of edge effects means that extrapolation to the special case of narrow buffer zones beside streams is difficult. Edge effects that strongly influence the abundance and distribution of the herb and shrub vegetation in the buffer zone may cause significant changes in the ecological services provided. These factors must be studied before solid recommendations on the width of upland vegetation required to form an effective buffer zone can be made.

Chapter 3: Trait Patterns and Plant Community Structure Across a Riparian Zone-Upland Ecotone

Introduction

Ecotones, or zones of rapidly changing vegetation, are complex and dynamic features of natural and human-altered landscapes (di Castri *et al.* 1988; Delcourt and Delcourt 1992; Risser 1995; Lachavanne 1997; Lloyd *et al.* 2000). In essence, an ecotone is a relatively small area of a landscape that experiences a rapid change in ecological structure and function relative to the landscape as a whole. It is typically associated with a discontinuity in one or more environmental factors or a change in the disturbance regime (Wiens *et al.* 1985; Hansen *et al.* 1992). Ecotones are of great interest to ecologists because they frequently support high biodiversity and have striking patterns of species distribution and community structure (e.g. Carter *et al.* 1994; Lachavanne 1997; Stohlgren and Bachand 1997; Lloyd *et al.* 2000). Ecotone-related research has many practical applications, including conservation biology (e.g. Matlack 1994b; Naiman and Décamps 1997; Williams-Linera *et al.* 1998), modeling the potential impacts of climate change (e.g. Nobel 1993; Lowell 2000), and in the formulation of ecological theory (e.g. Austin and Smith 1989; Auerbach and Schmida 1993).

An ecotone is characterized by changes in species composition and community structure. Four general patterns of change can occur across an ecotone (Figure 8). These patterns have typically been examined in terms of changes in species abundance or changes in environmental conditions. A wide range of other parameters also change across ecotones; they could be expected to follow similar patterns. Here we use species change as the measured parameter. Across any ecotone there will be two groups of species characteristic of each of the adjacent communities; species from these groups will change sharply in abundance across the ecotone and will only be abundant on one side. There will be a set of species that do not "notice" the ecotone and do not change significantly in abundance across it. A final group, the ecotone specialists, may be found peaking in abundance in the middle of the ecotone. Species from a variety of taxa

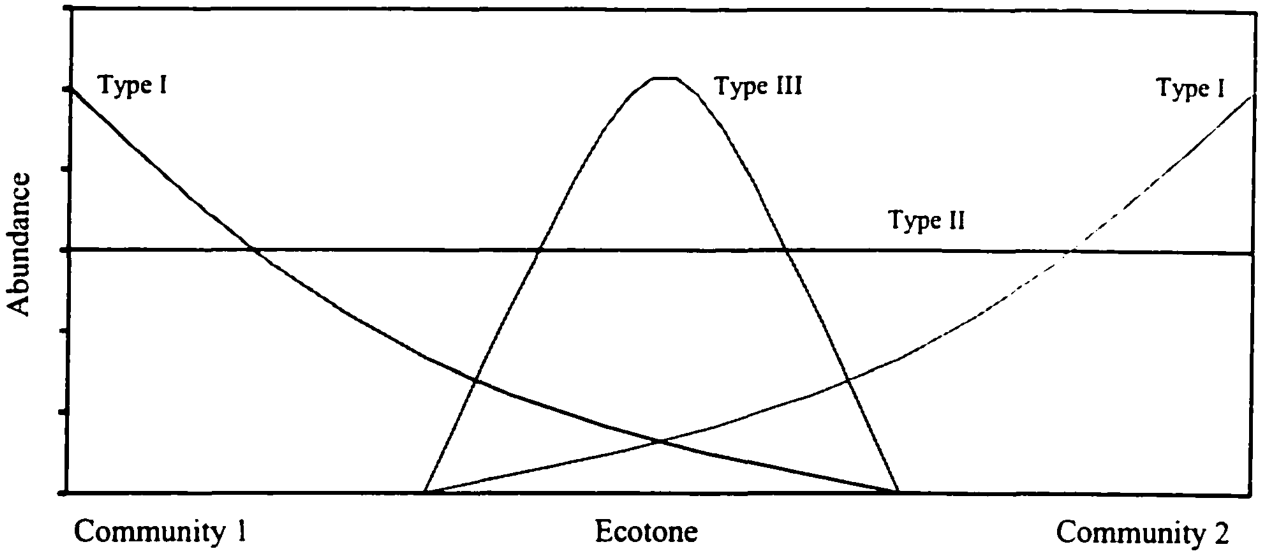

Figure 8: Three potential responses of species groups to a hypothetical ecotone. Type I species are confined to one side of the ecotone, Type II species do not "notice" the ecotone, and Type III species are ecotone specialists.

displaying all four of these responses are frequently observed at both habitat edges, or anthropogenic ecotones (e.g. Wales 1972; Williams-Linera *et al.* 1998), and natural ecotones (e.g. Carter *et al.* 1994; Stohlgren and Bachand 1997; Lloyd *et al.* 2000). These four groups are a simplification, as intermediate responses are likely to be found at any real ecotone, but the distinction gives a basis for the discussion and comparison of responses.

The rapid changes in community structure and species composition across the ecotone between two distinct communities provide an ideal setting to link the growing literature on ecotone dynamics to the large literature exploring the functional significance of individual plant traits. Papers considering the functional significance of one, or a small number of traits across a range of community types are common (e.g. Hughes *et al.* 1994; Leishman *et al.* 1995; Jackson *et al.* 1996). These analyses typically develop hypotheses on the functional links between trait patterns and community structure, however, they rarely evaluate how important a single trait may be relative to other traits in determining the overall structure of the plant community. A relatively new approach, the analysis of large matrices of plant traits, can accomplish this (e.g. Keddy 1992; Grime *et al.* 1997; Mabry *et al.* 2000). The process of constructing a trait matrix, exploring the relationships between traits, and finally making functional linkages between traits and the environment provides an attractive route to a general understanding of plant community structure and function (Keddy 1992). A multivariate analysis of a matrix of plant traits that includes information on how important a particular trait is in a community (e.g. Mabry *et al.* 2000) can assess the contribution of a particular trait to the overall community structure.

In this chapter I will follow the approach suggested by McIntyre *et al.* (1999) for analyzing a set of trait and vegetation data. I will look at a number of traits, both singly and all together across an abrupt ecotone, the riparian zone to upland transition found along small streams in northwestern Ontario. The rapid transition between the two very different vegetation types (Chapter 1) provides an ideal setting for a study of this type. The objectives for this study are a) to examine the overall trait structure across the ecotone, and b) to evaluate the patterns of change across the ecotone separately for each trait and to identify potential functional explanations for each pattern. This research will have implications for both our understanding of ecotone structure and for the methodology used in the analysis of trait matrices.

Methods

Study Area

The study was conducted in the boreal mixedwood forest near Thunder Bay, Ontario, Canada. The eighteen study sites were all located along small headwater streams (watersheds ranging in area from 100ha to 60000ha) without recent adjacent disturbance by either clear-cutting or forest fire. The riparian vegetation is heterogeneous, typically either a swamp thicket dominated by *Alnus incana*, or a sedge-dominated meadow marsh (Harris *et al.* 1996; Rankin 2000, Chapter 1). The riparian zones are variable in width (from 1m to 80m), and there is a characteristic shift in species composition from riparian specialist species at the streambank to a mixture of riparian and upland species at the riparian-upland ecotone. The riparian vegetation at each site is frequently a composite of the meadow marsh and swamp thicket vegetation, and there is very little systematic variation in the riparian zone community composition associated with watershed area (Chapter 1). Common riparian species in the study area include the shrubs *Alnus incana* and *Cornus stolonifera*, the sedge *Carex aquatilis*, the grass *Calamagrostis canadensis*, the herbs *Mertensia paniculata* and *Eupatorium maculatum*, and the pteridophyte *Athyrium filix-femina*. The upland forests are a range of boreal mixedwood and conifer-dominated stands typical of the southern boreal forest (Rowe 1972). The common upland understory species include the shrubs *Ledum groenlandicum* and *Acer spicatum*, the herbs *Cornus canadensis*, *Aster macrophyllus*, and *Aralia nudicaulis*, and the lycopods *Lycopodium annotinum* and *L. dendroideum*. The ecotone between the riparian zone and the upland forest is marked by a very rapid shift in species composition (Chapter 1).

Field Sampling

At each site species cover data were collected from four transects laid out across the riparian zone perpendicular to the stream. Two pairs of transects approximately 40m apart were placed on each side of the stream. On each transect one $1m^2$ quadrat was placed at the edge of the stream, one was placed directly on the ecotone between the riparian zone and the upland vegetation, and up to three quadrats, depending on riparian zone width, were spaced between the two across the riparian zone. At some transects the riparian zone was less than 1m wide; there the riparian zone and ecotone quadrats were eliminated prior to analysis. In each quadrat, the percent cover of all vascular plants was estimated by eye. Each transect was extended 30m into the upland where quadrats were placed at 10m, 20m, and 30m. The position of each quadrat relative to the stream and the riparian-upland ecotone were recorded, dividing the quadrats into eight groups.

Trait Matrix

Nine morphologic, reproductive, and physiologic traits were selected for inclusion in the matrix; they were all categorical variables with one to five categories in each (Table 11). Due to logistical limitations only a relatively small number of traits for which either information was readily available in the literature, or the species could be easily scored in the field for the trait were included. Fifty-one vascular plant species were included in the matrix. That number is only a proportion of the species found in the study area (Chapter 1), but it was impractical to include all of the rarer species. The species selected were those found in at least 10% of the quadrats either in the riparian zone or in the upland forest. The criteria used to score each trait are listed in Appendix 3, and the complete trait matrix and source references are presented in Appendix 4. The traits were coded as presence-absence dummy variables for analysis resulting in a 51 species x 26 trait matrix.

Table 11: List of traits and the categories of each trait included in the trait matrix. See Appendix 3 for the criteria used to score each trait.

Trait	Categories	Notes
Life-Form	Tree; Shrub; Herb; Graminoid; Pteridophyte	
Stem Tissue	Woody; Herbaceous	
Seed Dispersal Vector	Vertebrate; Wind; Water	Ingested and adhesive dispersal by vertebrates (van der Pijl 1969) are combined.
Pollination Vector	Insect; Wind; Self	
Seed Bank	Persistent; Transient	A persistent seed bank occurs when seeds can remain in the seed bank through a growing season.
Clonal Growth Form	Phalanx; Guerilla	A phalanx clone is tightly packed and excludes other clones, while a guerilla clone is typically loosely spaced and mixed with other clones of the same species (Lovett Doust 1981).
Clonal Growth Method	Rhizome; Resprout; Layer	Rhizomes here include morphologically distinct but functionally similar structures such as root suckers and stolons. Resprouting is growth from a previous root collar, and layering is adventitious rooting from a stem.
N-Fixation	Present/Absent	
Leaf Type	Deciduous; Evergreen	Evergreen leaves are photosynthetic organs that are produced in one growing season, maintained over a winter and used, even if only briefly, in the subsequent growing season (Chabot and Hicks 1982).
Potential Mycorrhizal Infection	Vesicular-Arbuscular Mycorrhizae; Ectomycorrhizae; Ericoid Mycorrhizae	

Data Analysis

The quadrat x species matrix of vegetation data were multiplied by the species x trait matrix to obtain a quadrat x trait matrix. The value in each cell of this matrix is the sum of the percent cover of each species observed in that quadrat that was positive for that trait. These values are a summary of the importance of each trait in each quadrat. All further analyses were carried out on this new matrix of 436 quadrats x 26 traits.

Principal Components Analysis (PCA) (Gauch 1982) was used to examine the overall trait structure of the community, and to identify relationships between traits. Broken-stick eigenvalues were used to determine the number of interpretable axes in the PCA output. To confirm that there were significant differences in trait structure across the riparian upland ecotone, a Multiple Response Permutation Procedure (MRPP) (Zimmerman *et al.* 1985) was used. The MRPP was used to test the null hypothesis of no difference in trait composition between the riparian, upland, and ecotonal communities. MRPP is a non-parametric analogue of Discriminant Function Analysis (DFA) that supports a multivariate test of the null hypothesis of no difference between *a priori* groups of samples. Both the MRPP and the PCA were performed using the PC-ORD ver.4 package (McCune and Mefford 1999).

Changes in the importance of individual traits over the ecotone were examined by plotting the mean value for each trait with 95% confidence interval error bars for each of the eight relative positions along the gradient. Relative position was used rather than distance *per se* due to the high variability of riparian zone widths in the study area (Rankin 2000; Chapter 1). To identify the traits with the largest changes in importance across the ecotone, the effect size was calculated from the ratio of the minimum and maximum mean importance values for each trait. Confidence intervals were calculated using SPSS ver. 9.0 (SPSS 1999).

Results

The overall trait structure of this plant community is dominated by four major axes of variation. The first four PCA axes (Figure 9), cumulatively accounting for 73.67% of the variation among the quadrats, are interpretable, as they all have eigenvalues higher than the broken-stick eigenvalues (Table 12). Eigenvectors for each trait on all four axes are presented in Table 13. A number of traits have relatively strong

Table 12: Eigenvalues, percent of variance explained, and broken-stick eigenvalues for the first four PCA axes. A broken-stick eigenvalue less than the calculated eigenvalue indicates an axis that explains a significant proportion of the variance in the data.

Axis	Eigenvalue	% Variance Explained	Broken-Stick Eigenvalue
1	9.563	36.782	3.854
2	3.760	14.460	2.854
3	3.533	13.590	2.354
4	2.297	8.836	2.021

Table 13: Trait eigenvector coefficients on the first four PCA axes.

Traits	Axis 1	Axis 2	Axis 3	Axis 4
Tree	-0.0080	-0.2040	-0.0265	-0.4472
Shrub	0.2744	-0.1310	-0.0533	0.0245
Herb	0.1208	0.1086	-0.3175	0.1891
Graminoid	-0.0047	0.4038	0.2226	-0.1953
Pteridophyte	0.1069	-0.0154	-0.0683	0.0433
Herbaceous Tissue	0.1318	0.4030	-0.0589	-0.0112
Woody Tissue	0.2659	-0.2067	-0.0810	-0.1382
Deciduous Leaves	0.2941	0.1734	-0.0565	0.0887
Evergreen Leaves	-0.0082	-0.2234	-0.1057	-0.4980
N-fixation	0.2279	-0.1130	0.2910	0.1112
Ectomycorrhizae	0.2424	-0.1778	0.1192	-0.0929
Ericoid Mycorrhizae	-0.0458	-0.1521	-0.1130	-0.2909
V-A Mycorrhizae	0.2803	0.0245	-0.0232	0.2056
Rhizome	0.2814	0.1771	-0.0651	0.0051
Resprouting	0.2824	-0.0815	-0.0411	0.0885
Layering	0.2278	-0.2704	0.1533	-0.0885
Wind Dispersal	0.2699	-0.0643	0.1413	-0.0704
Vertebrate Dispersal	0.0945	-0.0137	-0.4330	-0.0872
Water-Borne Dispersal	0.0184	0.3601	0.2051	-0.2623
Insect Pollination	0.1175	-0.0357	-0.4285	0.0475
Wind Pollination	0.2471	0.1118	0.2284	-0.1709
Self Pollination	0.0581	-0.0542	-0.1457	-0.0344
Phalanx Growth Form	0.2580	0.0762	0.2271	-0.0762
Guerrilla Growth Form	0.1070	0.2950	-0.3055	-0.1581
Long-Term Seed Bank	0.2689	-0.0750	-0.0035	0.1259
No Seed Bank	0.1054	0.2296	-0.1545	-0.3526

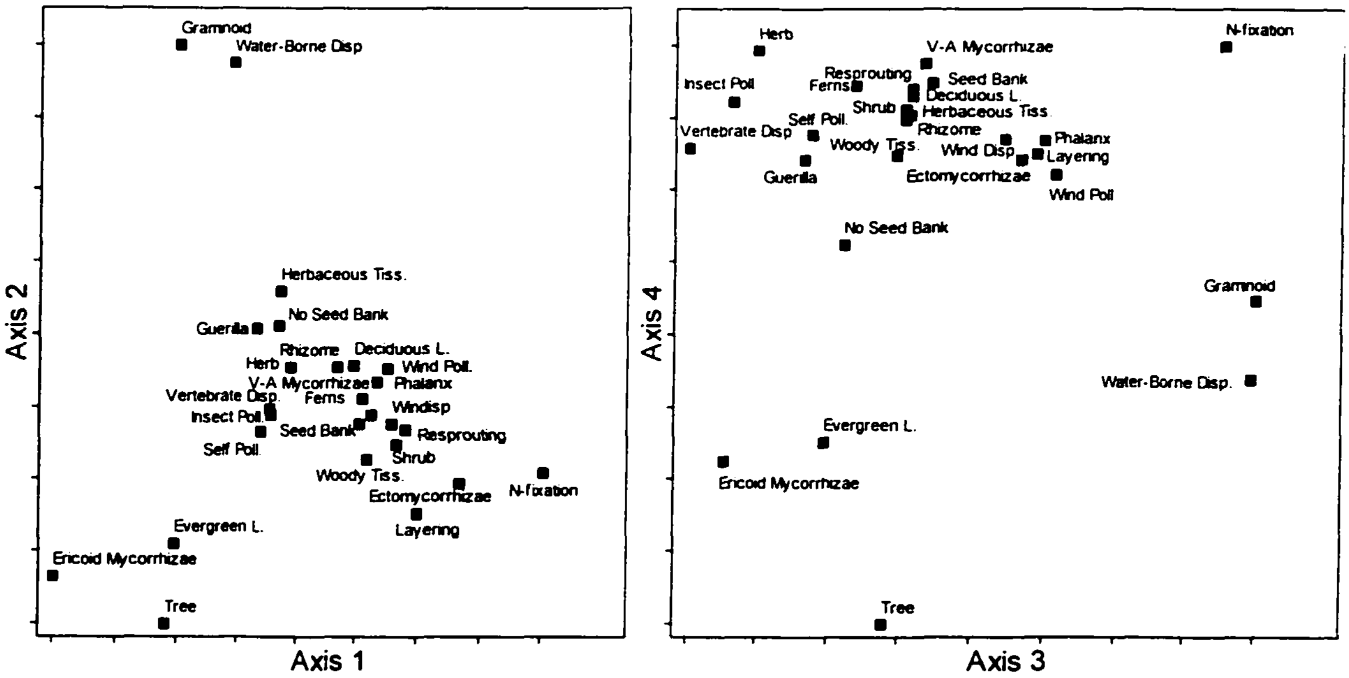

Figure 9: The first four axes from the trait ordination. Axis 1 separates traits associated with *Alnus incana* from traits not associated with that species. Axis 2 separates traits associated with *Calamagrostis canadensis* and *Carex aquatilis* from traits not associated with those species. Axis 3 separates traits associated with upland species (to the left of the figure) from riparian-associated traits (to the right). Axis 4 separates traits associated with species that possess V-A mycorrhizae from traits associated with species that do not.

positive eigenvector coefficients on the first axis, including the shrub life-form, woody tissue, deciduous leaves, nitrogen-fixation, V-A mycorrhizae, the resprouting, layering, and rhizomatous clonal growth methods, wind pollination, phalanx growth form, and seed banking ability. The second axis separates the tree growth form, woody tissue, evergreen leaves, and the layering habit from the graminoid life-form, herbaceous tissue, water-borne seed dispersal, guerilla growth form, and no long-term seed bank. These axes appear to be determined by the abundance in each quadrat of three species, the first by *Alnus incana*, and the second by *Carex aquatilis* and to a lesser extent by *Calamagrostis canadensis*. These species are the only ones in the data that had a large amount of their variation in abundance explained by one of the first two axes (r^2=0.509, 0.491, and 0.281 respectively), and they are three of the most abundant and important species in the riparian zone (Chapter 1). The third axis separates the herbaceous habit, vertebrate seed dispersal, insect pollination, and the guerilla clonal growth form from the graminoid life-form, nitrogen fixation, water-borne seed dispersal, wind pollination, and the phalanx growth form. The fourth axis separates the tree life-form, evergreen leaves, ericoid mycorrhizae, water-borne seed dispersal, and no long-term seed bank from V-A mycorrhizae. The third axis appears to weakly separate the riparian vegetation from the upland vegetation. The abundance of the important riparian species *Alnus incana* and *Carex aquatilis* are positively correlated with the third axis (r^2= 0.255 and 0.140 respectively), while common upland species such as *Aster macrophyllus, Diervilla lonicera,* and *Vaccinium myrtilloides* are negatively corellated with the third axis (r^2= 0.193, 0.152, and 0.100 respectively). The fourth axis appears to separate traits strongly associated with non-mycorrhizal, ectomycorrhizal or ericoid mycorrhizal status from the presence of V-A mycorrhizae.

The preceding ordination demonstrates that the abundance patterns of three dominant riparian species are responsible for the majority of the variation in trait structure. The riparian-upland ecotone, however, is the most striking discontinuity in species composition in the community. The MRPP demonstrates that there are significant differences in overall trait composition between the riparian, upland, and transitional quadrats (Table 14). The small A-value indicates that within each group quadrat composition is heterogeneous. The small p-value, however, indicates that the groups are significantly different, demonstrating that there is a significant difference in the trait makeup of the plant community found on each side of the ecotone. The ecotonal quadrats are intermediate between the communities on either side. This significant difference justifies the further exploration of trait patterns across the ecotone, even though much of the variation in the trait structure comes from other sources.

Table 14: Results of the MRPP testing the null hypothesis of no significant difference in trait composition between the riparian, transitional, and upland vegetation. Average distance is the mean Euclidean distance between each pairwise combination of quadrats from a particular microhabitat. N is the number of quadrats sampled in each microhabitat. The observed delta is calculated from the data while the expected delta is derived from a null distribution. T is the MRPP test statistic, and A is the chance corrected within-group agreement. The MRPP was highly significant (P<0.00000001).

Microhabitat	Average Distance	N	MRPP Statistics
Riparian	0.5000	148	Observed Delta= 0.4537
Transition	0.4722	73	Expected Delta = 0.5000
Upland	0.4156	215	T= -46.5762
			A= 0.0925

The patterns of changes in the importance of traits across the ecotone are variable (Figures 10-11; Table 15). Patterns of change that resemble the three patterns of change at the ecotone (Figure 8) are apparent. Traits that appear to match the Type I patterns include wind and insect pollination vectors, wind, vertebrate, and water dispersal vectors, the evergreen and deciduous leaf types, and the ability to fix atmospheric nitrogen. Traits that appear to match the Type II patterns include self-fertilization, most life-forms, the guerilla clonal growth form, and ecto- and ericoid mycorrhizae. Though the confidence interval bars overlap, there are traits that appear to have a Type III pattern including persistent soil seed banks, woody tissue, and the potential for vesicular-arbuscular mycorrhizal infection. Traits with a particularly strong effect size include the tree and graminoid life-forms, nitrogen fixation, ericoid mycorrhizae, and water-borne seed dispersal. Many of the traits with strong effect sizes, including graminoids, nitrogen fixation, and water-borne dispersal also have large eigenvector coefficients on the third PCA axis.

Table 15: Minimum, maximum, ratio of minimum to maximum, and mean 95% confidence interval for each trait across the riparian-upland ecotone. The min:max ratio is a measure of the "effect size", or the relative amount of change in a trait. The mean confidence interval is the mean of the confidence intervals from each of the eight relative positions across the gradient.

Traits	max value	min value	min:max	Mean 95% CI
Tree	8.22	0.52	15.91	2.28
Shrub	55.98	28.38	1.97	8.47
Herb	26.13	16.52	1.58	5.30
Graminoid	23.85	1.92	12.44	5.31
Pteridophyte	6.94	3.60	1.93	2.54
Herbaceous Tissue	50.04	26.03	1.92	6.36
Woody Tissue	60.61	36.98	1.64	8.61
Deciduous Leaves	92.73	48.25	1.92	9.09
Evergreen Leaves	16.71	3.90	4.28	3.60
N-fixation	31.60	4.40	7.19	6.47
Ectomycorrhizae	37.11	15.61	2.38	7.37
Ericoid Mycorrhizae	5.86	0.52	11.30	2.55
V-A Mycorrhizae	69.57	40.13	1.73	8.75
Rhizome	85.35	50.35	1.70	8.65
Resprouting	53.50	28.27	1.89	8.66
Layering	38.34	20.72	1.85	7.61
Wind Dispersal	58.48	25.01	2.34	7.93
Vertebrate Dispersal	39.93	17.08	2.34	6.73
Water-Borne Dispersal	16.28	1.44	11.27	4.59
Insect Pollination	47.06	26.78	1.76	6.87
Wind Pollination	65.06	22.15	2.94	7.56
Self Pollination	4.32	2.68	1.61	1.09
Phalanx Growth Form	75.96	27.83	2.73	8.27
Guerrilla Growth Form	50.65	37.91	1.34	7.35
Long-Term Seed Bank	67.68	37.65	1.80	8.76
No Seed Bank	39.15	23.97	1.63	6.98

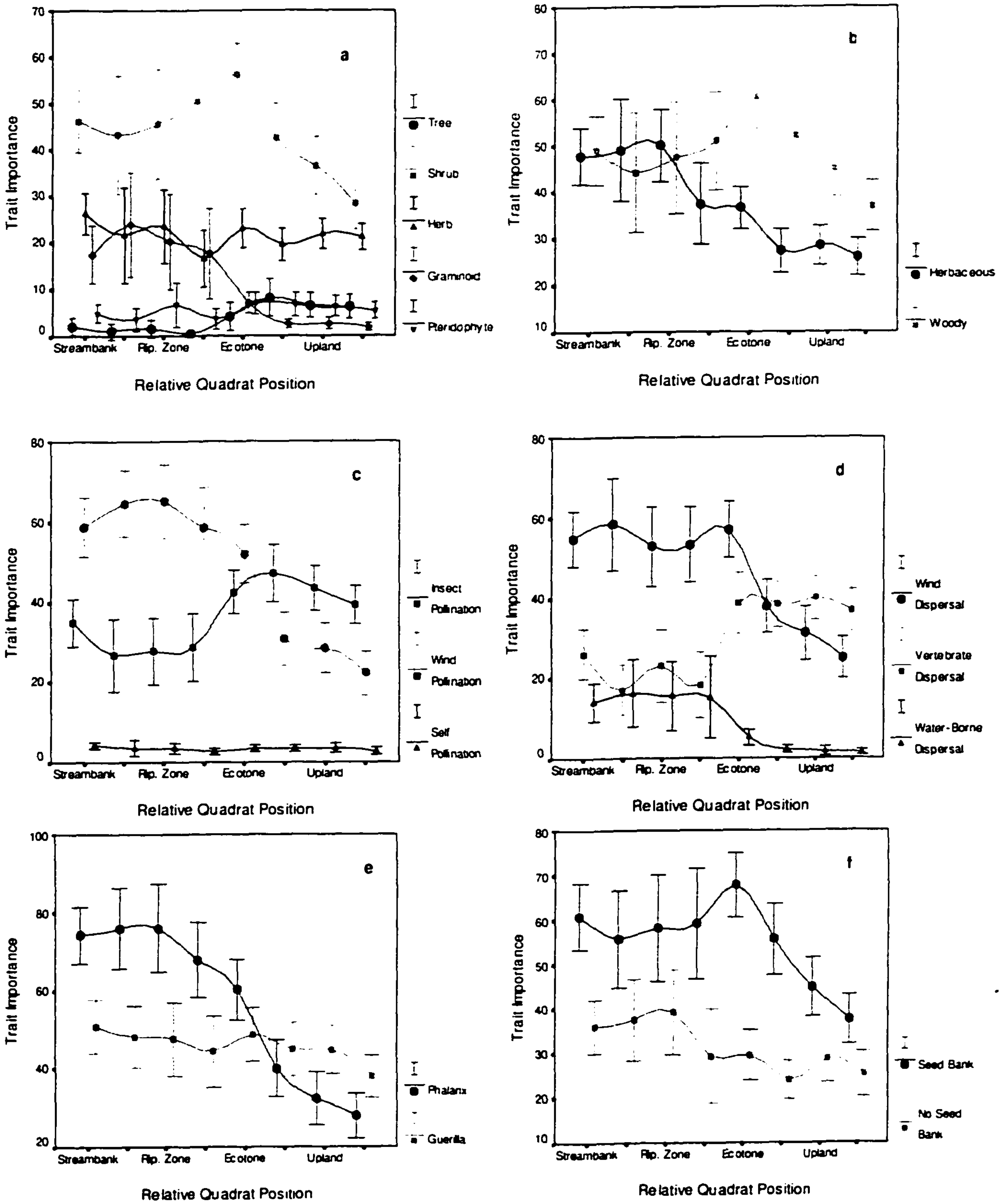

Figure 10: Changes in mean trait importance for a) the five life-forms, b) two plant tissue types, c) seed dispersal vector, d) pollination vector, e) clonal growth form, and f) seed banking trait. Error bars are 95% confidence intervals

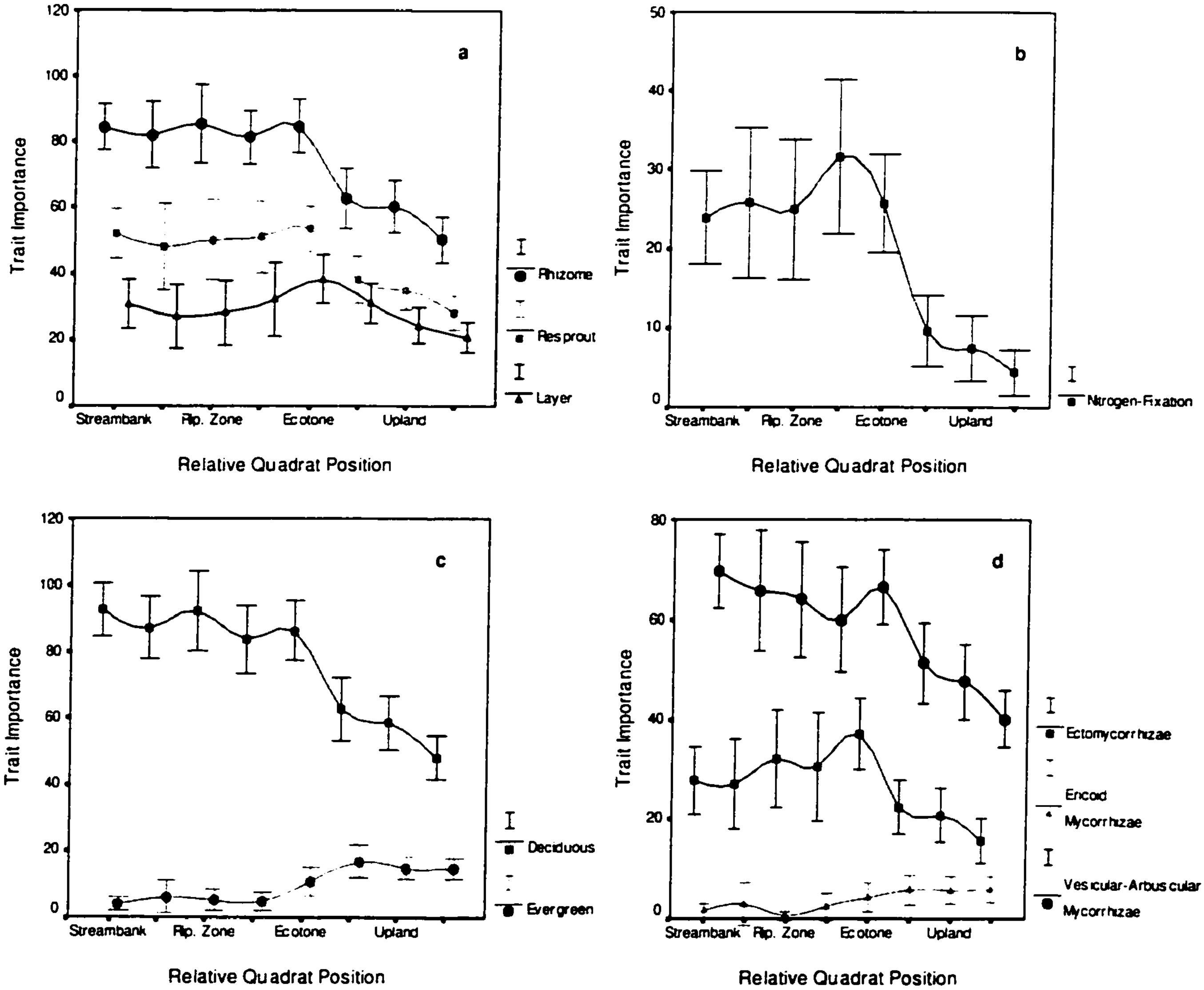

Figure 11: Changes in trait importance for a) clonal growth method, b) nitrogen-fixation traits, c) leaf type, and d) potential mycorrhizal infection traits. Error bars are 95% confidence intervals.

Discussion

Overall Trait Structure

The riparian, transitional, and upland quadrats are significantly different from each other as demonstrated by the MRPP, and the individual trait analyses have identified a wide range of trait patterns across the ecotone. These intuitively expected patterns, however, are not the primary force structuring these data. The PCA indicates that three common species contributing more to the variation in these data than the entire gradient of change in trait composition across the ecotone. The traits with similar eigenvector coefficients on the first axis are those for which *Alnus incana* is positive. The traits with similar coefficients on the second axis fall into two groups. The traits with positive coefficients are present in *Calamagrostis canadensis* and *Carex aquatilis* while the traits with negative coefficients are not present in those species. The division of traits along the third axis appears to separate traits found in many upland species from those important in the riparian zone. These traits and potential explanations for their patterns of importance across the ecotone are examined in more detail later in this discussion. The fourth axis separates groups of traits that rarely co-occur in the same species. The ordination diagrams in Figure 9 also reveals a number of interesting associations between individual traits. Some are clear-cut associations between a life-form and a trait present for phylogenetic or structural reasons in most or all representatives of that life-form. Examples of this include the association of shrubs with woody tissue and pteridophytes with wind dispersal.

These results indicate that multivariate analyses where species abundance data is used to weight trait data (e.g. Mabry *et al.* 2000) need to be evaluated carefully. It may also be important to consider whether rarer species should be included in the trait matrix. Collectively, those species make up a substantial proportion of the cover, even if they are not particularly important individually. The inclusion of the rare species would mean that the trait values would be relatively less weighted by the most abundant species, giving a better picture of the overall community trait composition. The importance of the three dominant species in the trait structure it likely a source of much of the variation apparent in the individual trait analyses.

The trait ordination reveals a wide range of interrelationships among diverse traits (Figure 9). Many are simply obvious correlations between life-forms and traits for which all species of the life-form are positive, but there are interesting functional interpretations that can be made for many of these relationships. For example, the traits for woody tissue and wind dispersal are relatively close together on the figure. It is clear that, since wind velocity is greatly decreased lower in the canopy (Hughes *et al.* 1994), it is adaptive to raise wind-dispersed seeds as high as possible. This normally requires strong stems, and hence woody tissue. The functional interpretations of other associations are not as apparent, for example the associations between the guerilla growth form and insect pollination and vertebrate dispersal on one hand and between the phalanx growth form with wind pollination and wind dispersal on the other. There are clearly many avenues to open to explore in the relationships among traits.

The Riparian-Upland Ecotone

The results of this study have demonstrated that an ecotone can be characterized not only as a discontinuity in either species abundance and distribution or in environmental conditions, but also as a discontinuity in the trait structure of a community. The trait patterns at the ecotone are similar to the hypothetical responses of species to an ecotone (Figure 8). The traits that appear to peak at the ecotone raise some especially interesting questions. Ecotonal species have been observed (e.g. Lloyd *et al.* 2000), so why not ecotonal traits? Are there traits that confer specific advantages to species in an ecotonal habitat, and equally, do ecotone-specialist species have unique complements of traits? Clearly there is much room for research on traits at ecotones.

The traits used in this matrix reflect aspects of the reproductive and spatial resource use strategies of plant species, however, flooding is clearly a critical factor in structuring the riparian vegetation at these sites (Naiman and Décamps 1997; Chapter 1). Unfortunately, no traits directly related to flooding tolerance could be included in the trait matrix for logistical reasons. A series of traits that accounted for the strategies commonly used by riparian species to withstand or avoid the effects of flooding (e.g. Blom and Voesenek 1996) would likely make the shift in trait structure across the ecotone much clearer. A comprehensive evaluation of a wide range of traits with potential influence at the riparian-upland ecotone would allow a much more complete understanding of the dynamics at the ecotone.

Life-form

The lack of Type I patterns in the importance of herbaceous plants, ferns and fern-allies, and woody shrubs across the ecotone (Figure 10) is not a surprise. Each of these life-forms is made up of a large number of species with a wide range of habitat preferences on both sides of the ecotone. The tree and graminoid life-forms have stronger changes in importance across the ecotone These life-forms are represented by relatively few species with more uniform habitat preferences than to the other groups. The shrub life-form appears to have a Type III response at the ecotone. This could be due to a weak edge effect, as shrub and understory cover is often higher at habitat edges (Murcia 1995).

Woody Tissue

There appears to be a decline in the importance of species with herbaceous tissue from the riparian zone to the upland, while woody species have a non-significant peak at the ecotone (Figure 10). The herbaceous plant pattern is interesting because it appears to have two distinct break points. The first is from high importance near the streambank to moderate importance within the riparian zone and at the ecotone, and the second decline to lower importance in the upland. Two factors are likely important here. First, there are many abundant riparian herb species primarily near the streambank; these species tend to decline rapidly in abundance within the riparian zone (Chapter 1). Second, the riparian zone in general has a higher herbaceous plant cover than the upland forest. The pattern of woody species mirrors the pattern found of the shrub life-form described in the previous section.

Seed Dispersal Vector

There appears to be a shift from wind to vertebrate seed dispersal vector from the riparian zone to the upland forest (Figure 10). This shift in dispersal vector is not surprising since it is well known that there are typically few wind-dispersed species in the forest understory (Howe and Smallwood 1982; Willson *et al.* 1990; Hughes *et al.* 1994). This pattern is likely due to limited wind penetration into the understory of closed canopy forests (Hughes *et al.* 1994). In contrast, the shrub thickets and meadow marshes of the riparian zone are fully exposed to winds, allowing for effective wind dispersal.

Given the apparent advantages of vertebrate dispersal in the upland forests, the presence of a number of common wind dispersed species, for example *Aster macrophyllus* and four species of *Lycopodium*, need to be explained. Willson *et al.*

(1990) put forward two hypotheses to explain the presence of species of this type. First, they suggest that fire, the dominant disturbance type in the boreal forest (Perera and Baldwin 2000), may select against vertebrate-dispersed species. They argue that after a large fire, seeds may need to disperse long distances to reach appropriate mineral soil seedbeds within the fire area, thus creating a selection pressure for wind-dispersed species. They also suggest that fire may reduce the number of vertebrate seed dispersers available. In a typical fire, however, there are frequent patches of residual vegetation (Eberhart and Woodward 1987) which can serve as seed sources. In addition, many boreal understory species have other attributes, such as deep rhizome systems, that allow them to survive most fires (McLean 1969; Flinn and Wein 1977; Mallik 1993). Some of these species, for example the vertebrate dispersed *Vaccinium myrtilloides*, produce their most abundant seed crops in the years following canopy opening events such as fire or clearcutting (Vander Kloet and Hall 1981; Moola and Mallik 1998). Vertebrate dispersal of seeds into burns is poorly studied, but it is important in some cases (Whelan 1986). In addition, it is well known that vertebrate dispersal vectors such as black bears (*Ursus americanus*) can be attracted from long distances to abundant food sources (Rogers 1987). Even if it is clear that selection against vertebrate-dispersed species cannot be universally implicated, many species have been observed to arrive in burns by wind (Mallik *et al.* 1984; Whelan 1986). This lends credence to the second hypothesis suggested by Willson *et al.* (1990), that some wind-dispersed species on forest floors may be relicts of earlier successional stages. Species such as *Aster macrophyllus* may initially establish following fire, but their long-lived and adaptive clonal habits allow them to survive into the subsequent closed-canopy forest.

Pollination Vector

There is a shift in the dominant pollination vector from wind in the riparian zone to insects in the upland forest (Figure 10). This pattern is in accord with the many studies that have found relatively little wind pollination in forested habitats (Bierzychudek 1982). In addition, Stebbins (1970) notes that evolutionary shifts from insect to wind pollination seem to occur in open habitats, suggesting strong selection for wind pollination in those habitats. As for dispersal vector, it is again likely that low wind penetration through the forest canopy makes wind an ineffective pollination vector for species in the understory. As further support for this hypothesis, several of the important insect pollinated species common in the riparian zone, including *Anemone quinquefolia* and *Mertensia paniculata*, are typically found under a dense canopy of *Alnus incana*.

Soil Seed Bank

There is a decrease in the importance of seed-banking species from the riparian zone to the upland forest, with an apparent peak at the ecotone (Figure 10). This pattern is in accord with other observations. Thompson *et al.* (1998) found that the mean seed longevity index is higher for wetland specialist species than for forest specialist species. The seed banks of temperate forests typically contain a large component of non-forest species, but relatively few seeds from forest-specialist species (Baskin and Baskin 1998; Bossuyt and Hermy 2001). In contrast, wetland seed banks can be large and are often be closely linked with the vegetation present (e.g. van der Valk 1981; Wilson *et al.* 1993).

The dominance of fire disturbance in the boreal forest (Perera and Baldwin 2000) may also be important in influencing this pattern. The predominantly deciduous vegetation of the riparian zone is much less flammable than the forested upland; fires typically stop at the ecotone resulting in a large difference in fire frequency and severity between the habitats (Chapter 2). Hughes *et al.* (1994) proposed that a seed bank is not an effective strategy in a fire-dominated community without a dispersal vector capable of deeply burying seeds. Species of *Viola* are the only ones in this community likely to employ ant dispersal (Beattie and Lyons 1975), the only reliable method of moving seeds deep into the soil (Hughes *et al.* 1994). This hypothesis needs further evaluation however, as seedlings emerging from the soil seed bank after fire are important in some ecosystems (e.g. Heinselman 1981; Mallik *et al.* 1984).

Clonal Growth Form

There is a decline in the importance of species that use the phalanx clonal growth form from the riparian zone to the upland, but there is no concurrent change in the importance of species using the guerilla form (Figure 10). The growth form of clonal plants is a response to many factors (Lovett Doust and Lovett Doust 1982; Hutchings and Bradbury 1986), but there may be a functional relationship between the decline in the phalanx growth form and the overstory conditions. Lovett Doust (1981) found that the guerilla species *Ranunculus repens* adopted a more extreme guerrilla form in woodland habitats when compared to open fields, possibly as a strategy to "seek" patches of sunlight. Similar behaviour has been observed in ericaceous shrub species (e.g. Bunnell 1990). Light conditions in the understory of the upland forest creates an environment that is much more patchy from the perspective of understory plants than that in the meadow marshes and alder thickets of the riparian zone. The probability of having at least one ramet of a clone exposed to higher light levels is important, as the reproductive success of understory herb species is often dependant on those high-light patches (Pitelka *et al.* 1980). Many of the important riparian species that use the phalanx growth form, for example *Alnus incana, Carex aquatalis, Eupatorium maculatum*, and *Myrica gale*, are found either in the upper vegetation layers or on the bank of the stream where they are exposed to full sunlight. In contrast, riparian guerilla species such as *Mertensia paniculata*, *Anemone quinquefolia, Phegopteris connectilis*, and *Lycopus uniflorus* are typically found under an *Alnus incana* canopy. Like all broad generalizations, however, this pattern has its exceptions, for example the guerilla shrub *Chamaedaphne calculata*, a species primarily found in open conditions.

Clonal Growth Method

There are a range of patterns in the methods used by plants for clonal growth (Figure 11). The importance of rhizomes and resprouting has a type I pattern with a decline from the riparian zone to the upland, while layering has an apparent Type III pattern. The decline in the importance of the resprouting method may be related to the similar decline in the phalanx growth form. Repeated resprouting from the same root collar is an ideal mechanism to produce a persistent phalanx growth form. Such an explanation is not applicable to the rhizomatous growth method. Rhizomes, stolons, and root suckers are used by many species from a wide range of habitats to produce both the phalanx and guerilla growth forms. Simple modifications of the distance between ramets and the angle and frequency of rhizome branching are sufficient to produce a wide array of growth forms (Bell and Tomlinson 1980). Layering is also a clonal growth method that is used by many species and can be adapted to produce a range of growth forms. Since layering species tend to be woody shrubs, it is likely that the non-significant peak in the layering trait at the ecotone is related to the similar peaks of the shrub life-form and woody tissue.

Nitrogen Fixation

There is a decline in the presence of species capable of hosting nitrogen-fixing bacteria from the riparian zone to the upland (Figure 11). This pattern is easily explained without invoking functional linkages. The two primary nitrogen-fixing species in northwestern Ontario, *Alnus incana* and *Myrica gale*, are typically found only in riparian habitats (Chapter 1). The shift in importance of this trait is likely only an artifact caused by the habitat preferences of the two dominant species. In addition, the values in the upland would be marginally higher if *Alnus viridis*, the third nitrogen-fixing species found in the study area, were included. That species is found in upland forest habitats in the study area but was not frequently encountered in this study and hence was not included in the analysis.

Leaf Type

There is a decline in the deciduous leaf type and a concurrent increase in evergreen across the ecotone (Figure 11). It is not immediately clear whether there should be a functional link between leaf type and habitat selection. Deciduous species tend to have higher rates of photosynthesis than evergreen species, but at a cost of lower nutrient-use efficiency, shorter growing season, and higher herbivory risk (Chabot and Hicks 1982; Aerts 1995; Landhäusser *et al.* 1997). Several hypotheses to explain the trade-offs between the evergreen and deciduous habitats have been considered (Chabot and Hicks 1982); two in particular may be relevant here. First, evergreen leaves are more efficient at retaining nutrients (Small 1972; Chabot and Hicks 1982), hence the higher photosynthetic potential of deciduous leaves may be an advantage in richer habitats, but not in nutrient poor habitats. Second, deciduous leaves, with their high photosynthetic rates tend to have lower water use efficiencies than evergreen leaves (Chabot and Hicks 1982); this may place deciduous species at an advantage in wetter habitats and evergreen in drier. Unfortunately, I do not have the data to further evaluate these hypotheses. I do not have any data on nutrient levels between the riparian and upland soils in the study area, though high nutrient levels are found in many riparian soils (Naiman and Décamps 1997). Similarly, the riparian zone is clearly wetter than the uplands but whether this moisture difference is influencing the pattern is unclear.

Mycorrhizal Status

There is a weak decline in the importance of VA- and ectomycorrhizae from the riparian zone to the upland, and a concurrent strong increase in the importance of ericoid mycorrhizae (Figure 11; Table 14). As well, both VA- and ectomycorrhizae have a potential Type III pattern at the ecotone. The patterns in the VA and ericoid mycorrhizae suggest similar relationships to those associated with the leaf-type patterns. It is well known that ericoid mycorrhizae tend to be found in soils with few available nutrients, and VA mycorrhizae in richer soils, with ectomycorrhizae intermediate (e.g. Read 1983; Allen 1991). The ectomycorrhizae do not conform to this pattern, but that may simply be an artifact of the sampling techniques used. The predominantly coniferous and ectomycorrhizal canopy trees in the uplands were not included in the data, artificially reducing the ectomycorrhizal importance values in that habitat. It is also likely that trends in the mycorrhizal spectrum of these communities are tied to soil conditions. Unfortunately, as for the leaf-type patterns, we do not have the soil nutrient data necessary to further evaluate the hypothesis.

The mycorrhizal status trait as applied in this study also raises some issues. The importance values for each type of mycorrhizae are not actual infection rates, but only the type of infection typically associated with each species. It is unknown whether or not the species are actually infected in these habitats or, if infected, the infection rates. It is likely that the actual infection rates in each species will vary widely between seasons and microhabitats. For example, in seasonally flooded habitats species may be non-mycorrhizal when the soils are saturated, but when the soil begins to dry out the plants can rapidly develop extensive mycorrhizae (Allen 1991). The role that such facultative infection could play in community differences across the ecotone is unknown. In a habitat like the riparian zone, a simple measure like the type of mycorrhizae is likely insufficient, and additional traits such as the intensity or seasonality of infection should be included.

Trait Selection

Finally, what implications do these results have for future applications of trait matrices? Keddy (1992) suggested that a large number of traits should be selected for this type of analysis because we currently do not know what patterns we should expect, and hence which traits should be chosen. Time and resources, of course, have a strong influence on the number and type of traits that can be included, so lists of traits must be limited. Weiher *et al.* (1999) suggested a core list of traits that could be used to ensure that the critical elements of a plant's life-history: dispersal, establishment, and persistence, are represented. This study highlights two additional issues. The use of traits with a) too low a "resolution" and b) a strong association with a small number of dominant species should be considered carefully. A trait such as life-form is useful because it can easily summarize the adaptations and behaviours of many species (Semenova and van der Maarel 2000). These variables are useful at a broad scale such as global vegetation patterns, but at the fine scale examined in this study the life-forms encompass too many species with divergent strategies to be useful. It may be appropriate in this situation to further subdivide the life-forms. The use of the nitrogen-fixing trait illustrates the second issue. In this study, nitrogen fixation was present in only two species that were predominantly found on only one side of the ecotone. This distribution pattern leads to an easily predicted pattern of limited explanatory power. When a trait is present in only a small number of species in the trait matrix, it is difficult to make an assessment of the functional importance of the trait. It is very difficult to separate the influence of that single trait on the abundance and distribution of species positive for it from all of the other traits that influence the habitat preferences of that species. In contrast, the patterns of traits such as dispersal or pollination vector lend themselves well to the search for functional linkages, as they are a summary of the behaviour of many species of diverse habitat preferences and trait compositions.

Another issue arises when multiple traits are used in a multivariate analysis where species abundance data is used to weight trait data. If a high-abundance species is positive for a trait then that trait may have a high loading on an axis. Such a result is to be expected, but may be erroneous if, even though the species is positive for the trait, the trait does not have a significant influence on the species' behaviour. A good example of this is the use of rhizomes or rhizome-like structures for clonal growth in *Alnus incana*. This behaviour has been observed in the species (Brown and Hansen 1954), but does not appear to be important in many populations (Huenneke 1987). Hence, the high positive loading of rhizomes on the first PCA axis is likely not a reflection of their importance in structuring the community. To correct this problem, it may be useful to include information on the relative importance of traits in the matrix.

Conclusion

This study has examined aspects of the community trait structure found at the riparian-upland ecotone along small streams in northwestern Ontario. The change in species composition that occurs within 1-2m at the ecotone is very abrupt, yet the majority of the variation in the community trait structure results from the distribution patterns of three common species in the riparian zone. The discontinuity in trait structure across the ecotone is apparent, however, with many traits changing in importance. There are functional explanations for many of these trait patterns found at the ecotone. These explanations can help to identify the environmental conditions responsible for structuring the vegetation in each community, and hence the factors that determine the position of the ecotone. This research suggests that there may be unique traits or complements of traits that confer advantages to species found in ecotonal habitats, adding another dimension to the long-standing search for ecotonal species.

General Discussion

This thesis has examined the vegetation ecology of the riparian zones of small headwater streams in northwestern Ontario. Many aspects of this vegetation were examined, including the biodiversity, distribution and abundance of species, the response to disturbances in the upland vegetation, and the trait dynamics at the riparian-upland ecotone. This general discussion will first highlight some key findings from each chapter and then will examine some unifying themes in the thesis.

The riparian zone vegetation of small streams in general, and in particular small streams in the boreal forest, have been very poorly studied (Hupp 1986). Without baseline data on biodiversity and species abundance and distribution, further research and objective evaluation of management programs are difficult. Several characteristics of the riparian zone plant community are described in Chapter 1. First, along the longitudinal gradient of watershed size beaver activity is a major factor influencing the distribution of meadow marsh vegetation (Naiman *et al.* 1988). Second, along the lateral gradient, the vegetation is remarkably homogenous with little evidence of the distinct bands of vegetation typically found within the riparian zones of larger streams (e.g. Wistendahl 1958; Lindsey *et al.* 1961; Bell and del Moral 1977; Hupp 1983; Bendix 1999). Third, there is a very distinct change in species composition associated with the riparian-upland ecotone. A number of indicator species useful in pinpointing the location of the ecotone are presented. These data form a basis for the subsequent analyses in this thesis and provide a baseline for future research on this vegetation type.

The impacts that a canopy-destroying disturbance in the upland forest can have on adjacent riparian zone vegetation are not well understood. The riparian zone provides many ecological services for the maintenance of stream water quality; any large changes in the riparian plant community may change the provision of those services. This has implications for the width of additional upland buffer that should be recommended in the provincial guidelines. In Chapter 2 the floristic composition was compared between riparian zones from undisturbed sites, sites with adjacent clear-cutting separated by a buffer zone, and sites where a forest fire had burned the canopy directly to the riparian-upland ecotone. No significant differences were found in overall community composition between the three disturbance types, though a small number of riparian-specialist herbs appeared to respond to higher light levels at the burned sites. These results suggest that the riparian zone vegetation is highly resilient to the kinds of changes in microclimate that occur following removal of the adjacent forest canopy (e.g. Brosofske *et al.* 1997). Instead, the riparian zone vegetation appears to respond primarily to stream-related factors such as flooding. This suggests that as long as the upland disturbances do not strongly change either the volume of water entering the stream or the flooding frequency there should be no major changes in the riparian zone vegetation. These results further suggest that aspects of the current management guidelines (Ontario Ministry of Natural Resources 1988) may need to be re-examined. If fish habitat protection is the main management goal, and if the riparian zone vegetation at a site can be demonstrated to provide all of the necessary ecological services to the stream, then additional upland buffers beyond the riparian zone may be unnecessary. If other management objectives are also important, for example the provision of habitat and movement corridors for bird species (e.g. Knopf and Samson 1994; Machtans *et al.* 1996), then upland buffers should be retained. As well, many streams have very narrow riparian zones that may not provide all of the necessary ecological services; these streams likely require some form of upland buffer. Research is needed on the form that these buffers should take.

Ecotones are recognized as an important feature of landscapes (e.g. di Castri *et al.* 1988; Delcourt and Delcourt 1992; Risser 1995; Lachavanne 1997; Lloyd *et al.* 2000), yet the enormous lengths of riparian-upland ecotone in the boreal forest have received very little attention. Ecotone research has tended to focus on either the distribution of species or fluxes of material across the ecotone. Examinations of the changes in plant traits or community structure across ecotones are less common, and no studies that I am aware of have examined changes in plant traits across ecotones. In Chapter 3, the changes in a range of plant reproductive, physiological, and morphological traits were examined across the abrupt ecotone. The patterns of trait distribution were used for hypothesis generation. The hypothetical functional interpretations of the trait patterns generated were evaluated against the available literature. As well, the overall changes in the trait structure of the plant community and some of the pitfalls of this type of trait analysis were examined. This study demonstrates the value of the trait matrix approach (Keddy 1992) both as a hypothesis generation tool, and for examination of the dynamics of plant communities across ecotones. This study demonstrates that the patterns of trait distribution across ecotones are similar to those that have been found for many species (e.g. Carter *et al.* 1994; Stohlgren and Bachand 1997; Lloyd *et al.* 2000). Finally, this study raises a fundamental question about the nature of ecotones. Many researchers have looked for ecotone-specialist species, and some have been identified (e.g. Lloyd *et al.* 2000). This study found weak evidence for some traits that appear to peak at ecotones. This raises two questions. First, whether there are certain traits that are found only at ecotones, and second whether the ecotone-specialist species that have been found have a unique complement of traits.

Beyond these key findings, a unifying theme through this thesis is the relationship between the disturbance regime and the biodiversity and species distribution and abundance at a site. It is well known that the disturbance regime is intimately linked to biodiversity, especially at an intermediate frequency and intensity (e.g. Connell 1978; Pickett 1980; Sousa 1984). In northwestern Ontario, there are three disturbances critical in structuring the riparian zone and adjacent upland vegetation: flooding, beaver activity, and fire. Flooding frequency and intensity structures the riparian zone vegetation along the lateral gradient and determines the position of the riparian-upland ecotone. Beaver activity and underlying factors that influence beaver habitat selection are responsible for much of the distribution of vegetation types along the longitudinal gradient. Fire structures the upland vegetation and influences the shifts in traits found at the riparian-upland ecotone. Consideration of the pattern of influence of each disturbance can help to determine the appropriate management regime.

The riparian zones along these streams lack the step-like geomorphology along the lateral gradient in these riparian zones found in other systems (e.g. Hupp and Osterkamp 1984; Osterkamp and Hupp 1985). This likely produces in a relatively smooth gradient of decreasing frequency and intensity of flooding across the riparian zone from the streambank to the riparian-upland ecotone. The only point on the lateral gradient with a strong change in vegetation, the riparian-upland ecotone, is likely the limit of annual flooding or saturated soils (Cowarden *et al.* 1979; Hupp and Osterkamp 1985).

The distinctiveness of the riparian-upland ecotone suggests that it should be used as the point of reference for management planning. This will help to resolve some ambiguity in the management guidelines (Ontario Ministry of Natural Resources 1988), which currently simply use the presence of woody vegetation to mark the beginning of the upland vegetation.

Much of the site to site variation along the longitudinal gradient appears to be the result of disturbance by beaver activity and by extension to geomorphologic features that influence beaver habitat selection. Silted-in beaver ponds initially develop to the *Calamagrostis canadensis* and *Carex aquatilis*-dominated meadow marsh vegetation and likely later to the *Alnus incana*-dominated swamp thickets. Anecdotal observations at the present study sites, including a fringe of *A. incana* around the edges of some meadow marshes and scattered individuals of *A. incana* apparently invading open areas in some marshes, suggest that over time the marshes may convert to swamp thicket. This successional pattern has been observed in other regions, but it is only partially understood, especially the interactions of multiple factors including beaver habitat selection and population dynamics over long time-scales (Naiman *et al.* 1988).

The switch in disturbance regimes from flooding to fire at the ecotone is apparent from the trait analysis. The decline of plant traits in the upland, such as the use of a long-term seed bank, appears to be related to the dominance of fire in that system. Similarly, the importance of the phalanx clonal growth form and water-borne seed dispersal in the riparian zone can be linked to the importance of flooding in that habitat. Other traits, such as the long-lived clonal growth habits displayed by almost all of the species in these communities are employed in different ways in each habitat to meet the particular challenges there. For example, species in the upland frequently resprout from root collars or deeply buried rhizomes as a strategy to survive fire (e.g. McLean 1969; Flinn and Wein 1977; Mallik 1993), while the dense mats of roots and rhizomes formed by many riparian species may be a strategy to prevent erosion and thus to avoid being washed away by floodwaters (e.g. Smith 1976). The trait analysis reveals the fundamental influences of different disturbance regimes in each habitat, but also the common threads of plant species using similar traits in very different ways to successfully establish and reproduce in their respective habitats.

The intersection of the three disturbance factors in the riparian zone and adjacent upland results in high biodiversity concentrated in a very small proportion of the total landscape. A major proportion of the vascular plant diversity in the Thunder Bay District is represented in these riparian zones, and many more species are found in the adjacent upland forest. It is likely that the full species richness of the areas falling within the 30-90m buffer guidelines along these streams (Ontario Ministry of Natural Resources 1988) would encompass the vast majority of the wetland and boreal forest species found in the district. This rich species diversity must be kept in mind when the management recommendations suggested in Chapter 2 are considered. These riparian zones and their adjacent upland buffers have a role and utility far beyond simple maintenance of stream water quality. The riparian buffer is an important habitat for a wide range of animal species (e.g. Machtans *et al.* 1996). As well, populations of upland plant species may be important source populations for the recolonization of clearcuts (e.g. Matlack 1994a; Brunet and von Oheimb 1998). Research on the stability of these buffer zones of upland vegetation, especially the influence of edge effects (Murcia 1995) on microclimate and species composition is needed.

Future Research Directions

This thesis has raised a number of research questions important to our understanding of the ecology and management of riparian zones. Research is needed to fill some gaps in our basic understanding of the ecology of these riparian zones in particular and ecotonal habitats in general. More importantly, there are elements of the current management strategy that still need to be critically evaluated. In conclusion, here are some of the specific research questions and directions raised in this thesis:

1) What are the successional relationships between the *Calamagrostis canadensis* and *Carex aquatilis*-dominated meadow marshes and the *Alnus incana*-dominated swamp thickets? How are these relationships influenced by geology, stream hydrology, and beaver population biology and habitat selection?

2) How do explicitly flooding-related plant traits such as aerenchyma tissue and metabolic adaptations help to make certain plant species competitive in the riparian environment, and how do these traits change in importance across the lateral gradient and at the riparian-upland ecotone?

3) Are there traits that are restricted to ecotonal environments? Do ecotone-specialist species have unique complements of traits?

4) What are the characteristics (extent, species composition, geomorphology etc.) of a riparian zone that is capable of providing all of the ecological services necessary for effective stream protection without an additional upland buffer? This subject will make clear the types of sites to which the recommendations in Chapter 2 may apply.

5) A buffer zone of upland vegetation may be required for some stream sites. Research is needed to determine the characteristics of effective upland buffers. Specific questions that need to be addressed may include:
   a) How extensive does an upland buffer need to be to provide effective protection of fish habitat when the riparian zone vegetation is narrow? Do the characteristics of these upland buffers need to vary with vegetation type and site conditions?
   b) What values do the upland vegetation in buffer zones have other than the protection of stream water quality? For example, is the wildlife habitat quality of a riparian zone enhanced by an upland buffer?
   c) What are the impacts of edge effects on the forest stands contained in buffer zones of upland vegetation? Do edge effects alter the effectiveness of an upland buffer?
   d) Are upland buffers important refuge habitats for plant species that cannot tolerate the abiotic conditions initially found in clearcuts? Are populations of these species important in subsequent re-colonization of these clear-cuts?

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Appendix 1: Site List

List of sites surveyed in this study. Watersheds are the major river drainage that the site is found in. UTM co-ordinates are in NAD-83 format. Notes refer to any unusual features or characteristics of the site.

Site	Watershed	Watershed Area Class	Disturbance Class	Watershed Area (ha)	UTM83_X	UTM83_Y	Notes
Walk 5.2	Mackenzie	100ha	Undisturbed	60	349948.15929	5389248.85186	
Walk 5.1	Mackenzie	100ha	Undisturbed	80	349699.71783	5388349.45627	
East Walk Trickle	Mackenzie	100ha	Undisturbed	80	354455.64361	5391116.77463	
Walk Mac 1K	Mackenzie	100ha	Undisturbed	90	357330.06250	5390568.50000	
East Walk Cold 1K	Mackenzie	100ha	Undisturbed	100	353549.78199	5389300.92760	
Moose Bones 1K	Mackenzie	100ha	Undisturbed	110	360305.59375	5395159.00000	
Walk 4.1	Mackenzie	100ha	Undisturbed	120	354400.42379	5394425.94492	Clear-cuts 50-70m past ends of upland transects to both sides of stream
East Walk 1k	Mackenzie	100ha	Undisturbed	120	353350.86235	5387350.25107	
Little 1K Twin	Mackenzie	100ha	Cut with Buffer	70	354703.84375	5389002.50000	Road runs parallel to right bank 30-40m away
Ravine 1K	Mackenzie	100ha	Cut with Buffer	70	364524.60794	5398849.97646	Stream in very steep ravine, clear-cuts to within 30m of banks on either side.
Log End 1K	Mackenzie	100ha	Cut with Buffer	70	356391.65625	5391843.00000	Variable buffer width, active channel disappears upstream of site
Walk Crown 3	Mackenzie	100ha	Cut with Buffer	90	351669.96214	5385122.47552	Machine damage on right bank in riparian zone downstream from sampling; complex secondary channels in riparian zone.

Site	Watershed	Watershed Area Class	Disturbance Class	Watershed Area (ha)	UTM83_X	UTM83_Y	Notes
Ezee1K	Mackenzie	100ha	Cut with Buffer	90	355827.46875	5390359.50000	Complex riparian zone because confluence with another stream occurs ~20m downstream from site
Walk Crown 1	Mackenzie	100ha	Cut with Buffer	120	351299.68823	5385700.72991	
Kevin's Mac 1k (M5.2)	Mackenzie	100ha	Cut with Buffer	150	363602.58800	5397143.37449	
Mid-Nonwatin	Nipigon Burn	100ha	Burn	160	382202.40625	5450313.50000	
Magee	Nipigon Burn	100ha	Burn	200	384423.96875	5449322.00000	
Setemio's 10 k	Mackenzie	1000ha	Undisturbed	740	364600.74100	5393023.83002	Side drainage enters on right bank
Wolf-10k	Wolf	1000ha	Undisturbed	1070	350968.25000	5416661.50000	Slow stream with partial beaver dams across streams; possibly a very old pond
Walk 6	Mackenzie	1000ha	Undisturbed	1130	349375.09884	5386927.62696	Beaver activity just downstream from site
Beck10K	Mackenzie	1000ha	Undisturbed	1250	360819.12500	5390996.50000	Very diverse riparian zone with complex side channels
Mack 5	Mackenzie	1000ha	Cut with Buffer	620	363922.08791	5397174.83242	
Mack L 10 k	Mackenzie	1000ha	Cut with Buffer	630	368753.25083	5401447.55258	Stream flows through rocky fissure; very narrow riparian zone.
M5 Wetland	Mackenzie	1000ha	Cut with Buffer	650	363547.58620	5397048.38618	
Walk Mac 10K	Mackenzie	1000ha	Cut with Buffer	770	357490.15625	5389299.00000	
Walk 5 (DN)	Mackenzie	1000ha	Cut with Buffer	1100	350175.29233	5388349.78063	Very wide riparian zone (78m) on right bank
Walk South (DS)	Mackenzie	1000ha	Cut with Buffer	1300	350099.74988	5388047.53608	Very diverse riparian zone
Larson Burn	Nipigon Burn	1000ha	Burn	440	389450.93750	5447240.00000	
Krutz Control	Nipigon Burn	1000ha	Burn	640	382024.31250	5449593.00000	
B. Sturgeon E. (mark	Nipigon Burn	1000ha	Burn	850	375376.09375	5467640.50000	

Site	Watershed	Watershed Area Class	Disturbance Class	Watershed Area (ha)	UTM83_X	UTM83_Y	Notes
B. Sturgeon E. (unmarked)	Nipigon Burn	1000ha	Burn	1000	376193.15625	5468302.00000	
Larson Burn 10 k	Nipigon Burn	1000ha	Burn	1070	389730.43750	5442838.00000	Beaver activity just upstream of site, some residual forest near riparian zone edge
Mack East (R2)	Mackenzie	3000-6000ha	Undisturbed	3500	364733.03235	5397429.55095	
Wolf West 50k	Wolf	3000-6000ha	Undisturbed	4030	356061.71875	5420829.50000	
Wolf East 50k	Wolf	3000-6000ha	Undisturbed	4140	357173.56250	5419087.50000	Very old logging close to stream on left bank
Walk Crown 5	Mackenzie	3000-6000ha	Undisturbed	4190	353327.62389	5385050.73997	
Walk Crown 6	Mackenzie	3000-6000ha	Undisturbed	4350	353699.89906	5385121.77281	
Eaglehead	Spruce	3000-6000ha	Undisturbed	4400	329179.37500	5425114.00000	Narrow riparian zone; old clear cuts (prob. 30+ yrs old) past ends of transects to both sides
Beck Clearcut	Mackenzie	3000-6000ha	Cut with Buffer	2690	361548.33194	5384596.14139	Clear-cuts to both sides of stream, buffers less than 30m wide
Abigogami 30k	Wolf	3000-6000ha	Cut with Buffer	2850	366540.68750	5425478.50000	Relatively old logging (at least 15yrs) close to right bank, Major windthrow patch in left bank upland
Walk 10	Mackenzie	3000-6000ha	Cut with Buffer	3260	351523.97695	5386575.77321	
Walkmac No-cut	Mackenzie	3000-6000ha	Cut with Buffer	3680	358298.50672	5383051.19979	

Appendix 2: Vascular Plant Species List

List of species observed in this study including accession numbers for voucher specimens in the Claude Garton Herbarium at Lakehead University (LKHD). Species observed in the riparian zone are noted, as are species that were lumped together.

Family	Species	Herbarium Assession #	Riparian	Notes
Equisetaceae	*Equisetum arvense* L.	n/a	Rip. Sp.	
	Equisetum sylvaticum L.	104334	Rip. Sp.	
Lycopodiaceae	*Lycopodium annotinum* L.	n/a	Rip. Sp.	
	Lycopodium clavatum L.	104278	Rip. Sp.	
	Lycopodium complanatum L.	104270		
	Lycopodium dendroideum Michx.	104274	Rip. Sp.	
	Lycopodium lucidulum Michx.	104479	Rip. Sp.	Added to *L. annotinum*
	Lycopodium selago L.	104471 104472 104473 104474 104475 104483	Rip. Sp.	Added to *L. annotinum*
Osmundaceae	*Osmunda claytoniana* L.	104281	Rip. Sp.	
	Osmunda regalis L.	104336	Rip. Sp.	
Dryopteridaceae	*Athyrium filix-femina* (L.) Roth	104408	Rip. Sp.	
	Dryopteris carthusiana (Vill.) H.P. Fuchs	104339	Rip. Sp.	Added to *D. expansa*
	Dryopteris expansa (C. Presl.) Fraser Jenk & Jeremy	104337	Rip. Sp.	
	Gymnocarpium dryopteris (L.) Newman	104319	Rip. Sp.	
	Matteuccia struthiopteris (L.) Todara	104273	Rip. Sp.	
	Onoclea sensibilis L.	104315	Rip. Sp.	
Thelypteridaceae	*Phegopteris connectilis* (Michx.) Watt	104340	Rip. Sp.	
Taxaceae	*Taxus canadensis* Marshall	104356	Rip. Sp.	

Family	Species	Herbarium Assession #	Riparian	Notes
Pinaceae	*Abies balsamea* (L.) Miller	n/a	Rip. Sp.	
	Larix laricina (Duroi) K.Koch	n/a	Rip. Sp.	
	Picea glauca (Moench) Voss	n/a	Rip. Sp.	
	Picea mariana (Miller) BSP	n/a	Rip. Sp.	
	Pinus banksiana Lambert	n/a	Rip. Sp.	
Cupressaceae	*Thuja occidentalis* L.	n/a	Rip. Sp.	
Sparganiaceae	*Sparganium emersum* Rehmann	104349	Rip. Sp.	Added to *Carex* Species Group #1
Alismataceae	*Sagittaria latifolia* Willd.	104257	Rip. Sp.	
Poaceae	*Agrostis scabra* Willd.	104406	Rip. Sp.	
	Brachyelytrum erectum (Shreb.) P.Beauv.	104263 104264 104265 104363 104364 104388 104389	Rip. Sp.	
	Bromus ciliatus L.	104279	Rip. Sp.	
	Calamagrostis canadensis (Michx.) P.Beauv	104255	Rip. Sp.	
	Cinna latifolia (Trevir. ex Goepponger) Griseb. in Ledeb.	104374	Rip. Sp.	Added to *C. canadensis*
	Elymus trachycaulus (Link) Gould in Schinn.	104482	Rip. Sp.	Added to *C. canadensis*
	Glyceria borealis (Nash) Batch.	104409	Rip. Sp.	Added to *C. canadensis*
	Glyceria canadensis (Michx.) Trin.	104327	Rip. Sp.	Added to *C. canadensis*
	Oryzopsis asperifolia Michx.	104347	Rip. Sp.	
	Phalaris arundinacea L.	104256	Rip. Sp.	Added to *C. canadensis*
	Schizachne purpurascens (Torrey) Swallen	104378	Rip. Sp.	
Cyperaceae	*Carex adusta* Boott	n/a		
	Carex aenea Fern.	104384		Added to *Carex* Species Group #1

Family	Species	Herbarium Assession #	Riparian	Notes
Cyperaceae	*Carex aquatilis* Wahlenb.	104387	Rip. Sp.	
	Carex arctata Boott	104441		
	Carex canescens L.	104382	Rip. Sp.	Added to *Carex* Species Group #2
	Carex crawfordii Fern.	104369	Rip. Sp.	Added to *Carex* Species Group #2
	Carex crinita Lam.	104350 104351	Rip. Sp.	
	Carex deflexa Hornem.	104377	Rip. Sp.	Several small forest floor *Carex* species likely included in this species
	Carex disperma Dewey	104376		
	Carex flava L.	104375	Rip. Sp.	Added to *Carex* Species Group #2
	Carex gracillima Schwein.	104410	Rip. Sp.	Added to *Carex* Species Group #1
	Carex houghtoniana Torrey ex Dewey	104383		
	Carex interior L. Bailey	104416		
	Carex intumescens Rudge	104322 104324	Rip. Sp.	Added to *Carex* Species Group #1
	Carex laxiflora Lam.	104413	Rip. Sp.	Added to *Carex* Species Group #1
	Carex leptalea Wahlenb.	104379	Rip. Sp.	Added to *Carex* Species Group #1
	Carex rostrata Stokes	104352	Rip. Sp.	
	Carex stipata Muhlen. Ex Wahlenb.	104353	Rip. Sp.	Added to *Carex* Species Group #1
	Carex trisperma Dewey	104415	Rip. Sp.	Added to *Carex* Species Group #2
	Carex vulpinoidea Michx.	104367	Rip. Sp.	Added to *Carex* Species Group #1
	Scirpus cyperinus (L.) Knuth	104261	Rip. Sp.	
	Scirpus hudsonianus (Michx.) Fern.	104310	Rip. Sp.	
Juncaceae	*Juncus brevicaudatus* (Engelm.) Fern	104390	Rip. Sp.	Analyzed as *Juncus* species
	Juncus effusus L.	104370	Rip. Sp.	Analyzed as *Juncus* species
	Juncus filiformis L.	104391	Rip. Sp.	Analyzed as *Juncus* species

Family	Species	Herbarium Assession #	Riparian	Notes
Juncaceae	*Juncus nodosus* L.	104368	Rip. Sp.	Analyzed as *Juncus* species
	Luzula acuminata Raf.	104304		
Liliaceae	*Clintonia borealis* (Aiton) Raf.	104335	Rip. Sp.	
	Maianthemum canadense Desf.	104320	Rip. Sp.	
	Streptopus roseus Michx.	104325	Rip. Sp.	
	Trillium cernuum L.	104331	Rip. Sp.	
Iridaceae	*Iris versicolor* L.	104300	Rip. Sp.	
Orchidaceae	*Cypripedium acule* Aiton	104282		
	Goodyera repens (L.) R.Br.	n/a		
	Listera cordata (L.) R.Br.	104385		
	Platanthera hyperborea (L.) Lindley	104360	Rip. Sp.	
Salicaceae	*Populus balsamifera* L.	n/a		
	Populus tremuloides Michx.	n/a	Rip. Sp.	
	Salix species	n/a	Rip. Sp.	Several species from genus likely present
Myricaceae	*Myrica gale* L.	104318	Rip. Sp.	
Betulaceae	*Alnus incana* (L.) Monech	104262	Rip. Sp.	
	Alnus viridis (Villars) DC.	104283	Rip. Sp.	
	Betula papyrifera Marshall	n/a	Rip. Sp.	
	Corylus cornuta Marshall	104297	Rip. Sp.	
Santalaceae	*Geocaulon lividum* (Richardson) Fern.	104381		
Polygonaceae	*Polygonum cilinode* Michx.	104311	Rip. Sp.	
Ranunculaceae	*Actaea rubra* (Aiton) Willd.	n/a	Rip. Sp.	
	Anemone quinquefolia L.	104305	Rip. Sp.	
	Aquilegia canadensis L.	104303	Rip. Sp.	
	Caltha palustris L.	104323	Rip. Sp.	

Family	Species	Herbarium Assession #	Riparian	Notes
Ranunculaceae	*Coptis trifolia* (L.) Salisb.	104321	Rip. Sp.	
	Thalictrum dasycarpum Fischer & Ave-Lall.	104316	Rip. Sp.	
Brassicaceae	*Cardamine pensylvanica* Muhlenb. ex Willd.	104354	Rip. Sp.	
	Erysimum cheiranthoides L.	104373		
Saxifragaceae	*Mitella nuda* L.	104291	Rip. Sp.	
Grossulariaceae	*Ribes glandulosum* Graur	104287	Rip. Sp.	
	Ribes hirtellum Michx.	104258	Rip. Sp.	
	Ribes triste Pall.	n/a	Rip. Sp.	
Rosaceae	*Amelanchier stolonifera* Wiegand	104341	Rip. Sp.	
	Fragaria virginiana Miller	104338	Rip. Sp.	
	Geum rivale L.	n/a	Rip. Sp.	
	Physocarpus opulifolius (L.) Maxim.	104301	Rip. Sp.	
	Potentilla fruticosa L.	104298	Rip. Sp.	
	Potentilla palustris (L.) Scop.	104293	Rip. Sp.	
	Prunus pensylvanica L.f.	104333	Rip. Sp.	
	Prunus virginiana L.	104309	Rip. Sp.	
	Rosa acicularis Lindl.	104326	Rip. Sp.	
	Rubus idaeus L.	n/a	Rip. Sp.	
	Rubus pubescens Raf.	104412	Rip. Sp.	
	Sorbus americana Marshall	104414	Rip. Sp.	*S. decora* also likely present, but flowering ind. were not found
	Spiraea alba Du Roi	104288	Rip. Sp.	
Polygalaceae	*Polygala paucifolia* Willd.	104344	Rip. Sp.	
Aceraceae	*Acer spicatum* Lam.	104313	Rip. Sp.	
Rhamnaceae	*Rhamnus alnifolia* L'Her.	104289	Rip. Sp.	
Hypericaceae	*Hypericum elipticum* Hook.	104362	Rip. Sp.	
	Triadenum fraseri (Spach) Gleason	104312	Rip. Sp.	

Family	Species	Herbarium Assession #	Riparian	Notes
Violaceae	*Viola adunca* Smith	104478	Rip. Sp.	Analysed as *Viola* species
	Viola cucullata Aiton	104477	Rip. Sp.	Analysed as *Viola* species
	Viola pubescens Aiton	104290	Rip. Sp.	Analysed as *Viola* species
	Viola renifolia A. Gray	104484	Rip. Sp.	Analysed as *Viola* species
Onagraceae	*Circaea alpina* L.	104280	Rip. Sp.	
	Epilobium angustifolium L.	104275	Rip. Sp.	
	Epilobium ciliatum Raf	104355	Rip. Sp.	
Araliaceae	*Aralia nudicaulis* L.	104296	Rip. Sp.	
Apiaceae	*Heracleum lanatum* Michx.	104302	Rip. Sp.	
	Sanicula marilandica L.	104285	Rip. Sp.	
	Sium sauve Walter	104358	Rip. Sp.	
Cornaceae	*Cornus canadensis* L.	104329	Rip. Sp.	
	Cornus stolonifera Michx.	104328	Rip. Sp.	
Pyrolaceae	*Moneses uniflora* (L.) A. Gray	104314		
	Orthilia secunda (L.) House	104295	Rip. Sp.	
	Pyrola elliptica Nutt.	104476	Rip. Sp.	
Monotropaceae	*Monotropa uniflora* L.	104380		
Ericaceae	*Gaultheria hispidula* (L.)Muhlenb. Ex Bigelow	n/a		
	Ledum groenlandicum Oeder	104346	Rip. Sp.	
	Vaccinium angustifolium Aiton	104345	Rip. Sp.	
	Vaccinium myrtilloides Michx.	n/a	Rip. Sp.	
Primulaceae	*Lysimachia thyrsiflora* L.	104386	Rip. Sp.	
	Trientalis borealis Raf.	104332	Rip. Sp.	
Oleaceae	*Fraxinus nigra* Marshall	n/a	Rip. Sp.	
Gentianaceae	*Gentiana rubricaulis* Schwein	104260	Rip. Sp.	
Menyanthaceae	*Menyanthes trifoliata* L.	n/a	Rip. Sp.	

Family	Species	Herbarium Assession #	Riparian Notes
Boraginaceae	*Mertensia paniculata* (Aiton) G. Don	104306 104307	Rip. Sp.
Lamiaceae	*Lycopus uniflorus* Michx.	104267	Rip. Sp.
	Mentha arvensis L.	104277	Rip. Sp.
	Scutellaria galericulata L.	104254	Rip. Sp.
Rubiaceae	*Galium trifidum* L.	104284	Rip. Sp.
	Galium triflorum Michx.	104292	Rip. Sp.
Caprifoliaceae	*Diervilla lonicera* Miller	104317	Rip. Sp.
	Linnaea borealis L.	104330	Rip. Sp.
	Lonicera canadensis Bartram	104299	Rip. Sp.
	Lonicera hirsuta Eaton	104286 104294	Rip. Sp.
	Lonicera involucrata (Richardson) Banks	104343	Rip. Sp.
	Lonicera villosa (Michx.) Roemer & Schultes	104259	Rip. Sp.
	Viburnum edule (Michx.) Raf.	104342	Rip. Sp.
Campanulaceae	*Campanula aparinoides* Pursh	104361	Rip. Sp.
Asteraceae	*Anaphalis margaritaceae* (L.) Benth & Hook.f. ex C.B. Clarke	104308	Rip. Sp.
	Aster ciliolatus Lindley	104365	Rip. Sp.
	Aster lateriflorus (L.) Britton	104348	Rip. Sp.
	Aster macrophyllus L.	104359	Rip. Sp.
	Aster modestus Lindley	104366	Rip. Sp.
	Aster puniceus L.	104266	Rip. Sp.
	Aster umbellatus Miller	104268	Rip. Sp.
	Cirsium muticum Michx.	104269	Rip. Sp.
	Erigeron strigosus Muhlemb. ex Willd.	104480	
	Eupatorium maculatum L.	104276	Rip. Sp.

Family	Species	Herbarium Assession #	Riparian	Notes
Asteraceae	*Euthamia graminifolia* (L.) Nutt.	104393	Rip. Sp.	
	Hieracium caespitosum Dumort.	104372	Rip. Sp.	
	Hieracium scabriusculum Schwein.	104481	Rip. Sp.	
	Lactuca biennis (Moench) Fern.	104357	Rip. Sp.	
	Petasites frigidus (L.) Fr.	n/a	Rip. Sp.	
	Prenanthes alba L.	104407		
	Solidago canadensis L.	104271	Rip. Sp.	Analyzed as *Solidago* species
	Solidago uliginosa Nutt.	104392	Rip. Sp.	Analyzed as *Solidago* species
	Sonchus asper (L.) Hill	104371	Rip. Sp.	

Appendix 3: Trait Criteria

Criteria used to determine which category each species should be placed in for each trait. When possible, each decision was based on literature sources for that species. Some categories were determined from personal observations or morphological descriptions with reference to lists of traits consistent with published syndromes. The full trait matrix and source references can be found in Appendix 4.

Trait	Categories	Notes
Life-Form	Tree	A woody species typically with only a single stem and adult height greater than 5m.
	Shrub	A woody species with single or multiple stems from single or multiple root collars and typically an adult height of less than 5m.
	Herb	A non-woody, non-graminoid angiosperm
	Graminoid	A member of the Cyperaceae, Poaceae, Juncaceae or Sparganiaceae families.
	Pteridophyte	A fern or fern-ally.
Stem Tissue	Woody/Herbaceous	Does the species have woody stem tissue?
Seed Dispersal Vector	Vertebrate	Fruits or seeds with adaptations such as fleshy fruit, bristles, or hooks consistent with the vertebrate-ingested or adhesive dispersal syndromes (van der Pijl 1969).
	Wind	Fruits or seeds with adaptations such as wings or a prominent pappus consistent with the wind dispersal syndrome (van der Pijl 1969), or minute spores.
	Water-borne	Fruits or seeds experimentally found to float for long periods or observed while floating.
Pollination Vector	Insect	Flowers observed to be attractive to insects and/or with a brightly-colored corolla or nectaries consistent with the insect pollination syndrome (Fægri and van der Pijl 1971).
	Wind	Flowers with adaptations such as feathery stigmas and reduced corolla consistent with the wind pollination syndrome (Fægri and van der Pijl 1971).
	Self	Species observed to self-pollinate and produce viable seed.

Trait	Categories	Notes
Seed Bank	Persistent	When seeds from a previous growing season remain viable after at least one subsequent season (Baskin and Baskin 1998). Thompson and Grime (1979) provide a list of some seed traits consistent with persistent seed banks that were used to score some species.
	Transient	When seeds can only remain viable in the soil from the end of one growing season to the beginning of the next (Baskin and Baskin 1998).
Clonal Growth Form	Phalanx	Species where clone ramets are often tightly packed, the clone grows along a "front", and typically other clones of the same species are excluded (Lovett Doust 1981).
	Guerilla	Species where clone ramets are typically loosely spaced, the clone "explores" widely spaced patches, and is found mixed with other clones of the same species (Lovett Doust 1981).
Clonal Growth Method	Rhizome	A distinct structure that extends some distance from the parent ramet to a position where a daughter ramet is produced. This includes true rhizomes and morphologically distinct but functionally similar structures such as root suckers and stolons.
	Resprouting	growth of a new ramet from an existing root collar
	Layering	adventitious rooting from a stem or branch
N-Fixation	Present/Absent	The presence or absence of root nodules that are known to harbour nitrogen-fixing bacteria
Leaf Type	Deciduous	Photosynthetic organs that are produced in one growing season and only photosyntheticly active over that season.
	Evergreen	Photosynthetic organs that are produced in one growing season, maintained over a winter and photosyntheticly active, even if only briefly, a subsequent growing season (Chabot and Hicks 1982).
Potential Mycorrhizal Infection	Vesicular-Arbuscular Mycorrhizae; Ectomycorrhizae; Ericoid Mycorrhizae	Species are scored as present for a type of mycorrhizal infection if species has been observed to be infected under field conditions, or if the consensus in the literature is that the species, genus, or family is commonly infected.

Appendix 4: Trait Matrix

In this appendix, the raw trait matrix and associated source references are presented. Notes necessary for interpretation of the matrix can be found on page121. Details of how species were scored for particular traits can be found in Appendix 3. Additional traits for which information was incomplete and for species that were not included in the analysis are available on request from the author.

References are as follows: (1) Ahlgren 1960, (2) Anderson and Louks 1973, (3) Antos 1988, (4) Antos and Zobel 1984, (5) Archibold 1979, (6) Baldwin and Sims 1997, (7) Bawa *et al.* 1982, (8) Beattie 1969, (9) Bell 1991, (10) Beresford-Kroeger 2001, (11) Bernard 1990, (12) Brundrett and Kenderick 1988, (13) Burns and Honkala 1990, (14) Calmes and Zasada 1982, (15) Cody and Britton 1987, (16) Densmore and Zasada 1977, (17) Dore and McNeill 1980, (18) Dyer and Lindsay 1992, (19) Edwards 1984, (20) Eriksson 1989, (21) Faegri K and van der Pijl 1971, (22) Fyles 1989, (23) Gerdemann 1968, (24) Gleason 1963, (25) Gorham and Somers 1973, (26) Granstrom 1982, (27) Grime *et al.* 1988, (28) Haeussler and Coates 1986, (29) Hall *et al.* 1979, (30) Harley and Harley 1987, (31) Heinrich 1976, (32) Hiirsalmi 1969, (33) Hudson 1959, (34) Huenneke 1987, (35) Kramer and Johnson 1987, (36) Landhäusser *et al.* 1997, (37) Legere and Payette 1981, (38) Lovell 1900, (39) Mahall and Bormann 1978, (40) Mallik *et al.* 1997, (41) Malloch and Malloch 1981, (42) Malloch and Malloch 1982, (43) Matlack and Good 1990, (44) Mladenoff 1990, (45) Morris 1996, (46) Mulligan and Munro 1981, (47) Pitelka *et al.* 1985, (48) Pojar 1974, (49) Post 1965 , (50) Powelson and Lieffers 1991, (51) Primack 1973, (52) Qi and Scarratt 1998, (53) Raven *et al.* 1992, (54) Read *et al.* 2000, (55) Reader 1975, (56) Reader 1977, (57) Regal 1982, (58) Ridley 1930, (59) Ringus and Sims 1997, (60) Rodriguez-Barrueco 1969, (61) Rose 1980, (62) Rygren and Hestmark 1997, (63) Schoen 1977, (64) Schopmeyer 1974, (65) Shaver *et al.* 1979, (66) Shirreffs 1985, (67) Silva *et al.* 1982, (68) Sims *et al.* 1990, (69) Skene *et al.* 2000, (70) Small 1976, (71) Smith 1962, (72) Sobey and Barkhouse 1977, (73) Sopar and Heimburger 1982, (74) Tappeiner 1971, (75) Thaler and Plowright 1980, (76) Thompson and Plowright 1980, (77) USDA, NRCS 2001, (78) USDA, Forest Service 2001, (79) Vander Kloet 1976, (80) Vander Kloet and Hall 1981, (81) van der Pijl 1969, (82) Wesley *et al.* 1986, (83) Whitney 1986, (84) Wilson *et al.* 1993, (85) Yorks *et al.* 2000.

Species	Life-Form	Woody Tissue	Leaf Type	N-fixation	Mycorrhizal Status	Seed Bank	Dispersal Vector	Pollination Vector	Method Clonal Growth	Clonal Growth Form
Abies balsamea	T	W	E^{6}	$A^{13\ 60\ 77}$	$Ec^{30C\ 41}$	$A^{9\ 68\ 77}$	$W\ V^{13}$	$W^{13\ 64\ 68}$	L^{9}	P^{9J}
Acer spicatum	S	W	D^{6}	$A^{60\ 77}$	$V\text{-}A^{30B\ 41}$	P^{52}	$W^{9\ 64}$	$I\ W^{31\ 57}$	$L\ Rh\ Sp^{9}$	P^{49}
Alnus incana	S	W	D^{6}	$P^{59\ 60\ 77}$	$Ec\ V\text{-}A^{41}$	P^{77A}	$W^{9\ 64}$	$W^{9\ 31}$	$L\ Rh\ Sp^{9}$	P^{34}
Amelanchier species	S	W	D^{6}	$A^{9\ 60}$	$V\text{-}A^{41B}$	A^{9}	$V^{9\ 64}$	I^{31B}	$Rh\ Sp^{9}$	P^{9}
Anemone quinquefolia	H	H	D^{T}	A^{60}	$V\text{-}A^{30B}$	$A^{66B,P}$	$U^{66B,M}$	I^{48B}	Rh^{24}	G^{S}
Aralia nudicaulis	H	W	$D^{7\ 36\ 77}$	$A^{60\ 77}$	$V\text{-}A^{41}$	P^{77}	V^{19}	$I^{7\ 31\ 75}$	$Rh^{72\ 77}$	G^{19}
Aster macrophyllus	H	H	D^{77A}	$A^{60\ 77A}$	$V\text{-}A^{42}$	P^{77A}	$W\ V^{1\ 24H}$	I^{24I}	$Rh^{24\ 77A\ S}$	G^{S}
Aster puniceus	H	H	D^{77A}	$A^{60\ 77A}$	$V\text{-}A^{30B}$	A^{77A}	W^{24H}	I^{24I}	Rh^{77A}	$G\ P^{S}$
Aster umbellatus	H	H	D^{T}	A^{60}	$V\text{-}A^{30B}$	A^{P}	W^{24H}	I^{24I}	Rh^{S}	$G\ P^{S}$
Athyrium filix-femina	P	H	$D^{15\ 24}$	$A^{60\ 77}$	$V\text{-}A^{27\ 30}$	$P^{18E\ 62}$	$W^{27\ 58}$	N^{53}	$Rh^{28\ 77\ S}$	P^{S}
Betula papyrifera	T	W	D^{6}	$A^{9\ 60\ 77}$	Ec^{68}	$P^{68\ 77}$	$W^{1\ 13}$	$W^{31\ 68}$	$L\ Rh^{9}$	P^{28}
Calamagrostis canadensis	G	H	D^{77}	$A^{9\ 60\ 77}$	$V\text{-}A^{42}$	P^{9}	$W^{1\ 9}$	$W^{9\ 21G}$	$Rh^{9\ 77}$	$G\ P^{28\ 50}$
Campanula aparinoides	H	H	D^{77}	$A^{60\ 77}$	$V\text{-}A^{30B}$	$A^{27\ 77}$	W^{58B}	$I^{24I\ 27}$	Rh^{77}	G^{S}
Carex aquatilis	G	H	$D^{25\ 65\ 77}$	$A^{60\ 77}$	N^{42G}	A^{77}	$H^{58C,K}$	W^{21G}	$Rh^{11C\ 65}$	$G\ P^{S}$
Carex deflexa	G	H	D^{T}	A^{60}	$N^{23\ 30D\ 42G}$	$P^{O,P}$	$H^{58C,K}$	W^{21G}	$Rh^{11C\ S}$	P^{S}
Chamaedaphne calculata	S	W	E^{6}	$A^{60\ 77}$	$Er^{13\ 42}$	A^{77}	W^{73H}	$I^{31\ 55\ 56\ 70}$	$Rh\ Sp^{77}$	G^{S}
Cirsium muticum	H	H	E^{27B}	A^{60}	$V\text{-}A^{30B}$	P^{27B}	W^{24H}	I^{24I}	N^{77}	N^{77}
Clintonia borealis	H	H	D^{47}	$A^{60\ 77}$	$V\text{-}A^{41}$	$A^{44\ 52\ 77}$	V^{1}	$I^{76\ 31\ 75}$	$Rh^{47\ 77}$	P^{20}
Coptis trifolia	H	H	E^{6}	A^{60}	$V\text{-}A^{41}$	A^{52}	U^{Q}	I^{48}	$Rh^{72\ S}$	G^{S}
Cornus canadensis	H	H	D^{36}	$A^{60\ 77}$	$V\text{-}A^{41}$	$P^{5\ 77}$	$V^{1\ 64\ 81}$	$I^{48\ 75}$	$Rh\ Sp^{77}$	G^{S}
Cornus stolonifera	S	W	D^{6}	$A^{9\ 60\ 77A}$	$V\text{-}A^{42}$	$P^{9\ 35}$	$V^{9\ 64\ 81}$	I^{75}	$L\ Rh\ Sp^{9\ 77}$	$G\ P^{59}$
Corylus cornuta	S	W	D^{6}	$A^{60\ 77}$	Ec^{42}	$A^{5\ 52\ 77}$	$V^{1\ 64\ 81}$	W^{31}	$Rh\ Sp^{77}$	G^{74}
Diervilla lonicera	S	W	D^{6}	$A^{60\ 77}$	$V\text{-}A^{41}$	P^{77}	U^{Q}	$I^{31\ 38A\ 63\ 76}$	$Rh\ Sp^{63\ 77}$	G^{S}
Dryopteris expansa	P	H	$E^{12B\ 39B}$	A^{60}	$V\text{-}A^{12B\ 27}$	$P^{62(\text{weak})\ 71}$	W^{27B}	N^{53}	Rh^{72}	P^{S}
Eupatorium maculatum	H	H	D^{T}	A^{60}	$V\text{-}A^{30B}$	$P^{O.P}$	W^{24H}	$I^{10\ 24I}$	Rh^{S}	P^{S}

Species	Life-Form	Woody Tissue	Leaf Type	N-fixation	Mycorrhizal Status	Seed Bank	Dispersal Vector	Pollination Vector	Method Clonal Growth	Clonal Growth Form
Galium triflorum	H	H	D^{T}	A^{60}	V-$A^{12B\ 42}$	P^{35}	V^{24H}	I^{24I}	Rh^{S}	G^{S}
Ledum groenlandicum	S	W	E^{6}	$A^{60\ 77}$	$Er^{13\ 41}$	$P^{14\ 26B\ 77}$	W^{73H}	$I^{9\ 31\ 48\ 55\ 56}$	$L^{9\ 14}$	G^{20}
Linnaea borealis	S	W	E^{6}	A^{60}	V-$A^{30\ 41}$	$P^{62\ (weak)}$	V^{73}	$I^{38\ 48}$	$L^{20\ S}$	$G^{4\ S}$
Lycopodium annotinum	P	H	E^{6}	$A^{60\ 77}$	N V-$A^{42D\ 54C,D}$	A^{26}	$W^{53\ 58}$	N^{53}	L $Rh^{20\ 51}$	$G^{20\ 51}$
Lycopodium dendroideum	P	H	E^{15}	A^{60}	N V-$A^{42A,D\ 54C,D}$	A^{26}	$W^{53\ 58}$	N^{53}	Rh^{S}	$G^{51A\ S}$
Lycopus uniflorus	H	H	D^{T}	A^{60}	V-A^{30B}	P^{27B}	H V^{27B}	I^{24I}	Rh^{24}	G^{S}
Maianthemum canadense	H	H	D^{67}	A^{60}	V-A^{41}	$A^{44\ 85}$	$V^{1\ 24H}$	$I^{31\ 67\ 75}$	$Rh^{67\ 72\ S}$	G^{S}
Mentha arvensis	H	H	D^{77}	$A^{60\ 77}$	V-A^{30}	$P^{5\ 27}$	H^{27}	I^{24I}	Rh^{S}	G^{S}
Mertensia paniculata	H	H	D^{T}	A^{60}	V-A^{30G}	A^{P}	U^{Q}	I^{45}	Rh^{S}	G^{S}
Mitella nuda	H	H	E^{T}	A^{60}	N^{42}	P^{P}	U^{R}	$W^{T,I}$	Rh^{24}	P^{S}
Myrica gale	S	W	$D^{24\ 77}$	$P^{60\ 61\ 77}$	V-$A^{30\ 61}$	$A^{77\ 84}$	H $W^{58\ 69}$	W^{24I}	Sp $Rh^{77\ 69}$	P^{69}
Oryzopsis asperifolia	G	H	E^{17}	A^{60}	V-A^{41}	P^{22B}	U^{1}	$W^{T,I}$	Rh^{S}	P^{S}
Phegopteris connectilis	P	H	D^{15}	A^{60}	V-A^{30}	P^{62}	W^{53}	N^{53}	Rh^{S}	G^{S}
Picea mariana	T	W	E^{6}	$A^{13\ 60\ 77}$	$Ec^{42\ 68}$	P^{9}	$W^{13\ 68}$	W^{68}	$L^{9\ 37}$	P^{37J}
Prunus virginiana	S	W	D^{6}	$A^{9\ 60\ 77}$	$N^{41\ 42L\ 46}$	P^{77}	$V^{64\ 46}$	$I^{31\ 46\ 64}$	Rh $Sp^{9\ 40\ 46\ 77}$	G^{40}
Ribes triste	S	W	D^{6}	A^{60}	V-$A^{12B\ 27B\ 30B}$	P^{35B}	V^{64C}	$I^{T,I}$	L $Sp^{28B\ S}$	G^{S}
Rosa acicularis	S	W	D^{6}	$A^{9\ 60\ 77}$	$N^{30B\ 42}$	$P^{9\ 77}$	$V^{1\ 9\ 16}$	I^{9}	Rh $Sp^{9\ 14\ 77}$	G^{14}
Rubus idaeus	S	W	D^{6}	$A^{9\ 60}$	N^{42}	$P^{9\ 26\ 62\ 83\ 85}$	$V^{1\ 9\ 83}$	$I^{9\ 31}$	Rh Sp^{33}	G P^{33}
Rubus pubescens	S	W	$D^{6\ 36}$	A^{60}	N^{42}	A^{83}	$V^{1\ 83}$	$I^{T,I}$	Rh^{S}	G^{S}
Scirpus cyperinus	G	H	D^{77}	$A^{60\ 77}$	N^{42G}	$P^{43\ 44B\ 77\ 84}$	U^{N}	W^{24I}	Rh^{S}	P^{S}
Streptopus roseus	H	H	D^{T}	A^{60}	V-A^{42}	A^{44}	V^{24H}	$I^{T,I}$	$Rh^{72\ S}$	$G^{3\ S}$
Thalictrum dasycarpum	H	H	D^{T}	A^{60}	V-A^{30B}	A^{44}	W^{81C}	W^{21C}	Sp^{S}	P^{S}
Trientalis borealis	H	H	D^{2}	A^{60}	V-$A^{32B\ 41}$	P^{32F}	U^{32B}	$I^{15\ 32B}$ 6^{7}	Rh^{2}	G^{20}
Vaccinium angustifolium	S	W	D^{6}	$A^{60\ 77}$	$Er^{13\ 42}$	P^{82}	$V^{1\ 9\ 29\ 79}$	$I^{9\ 29\ 31}$	Rh $Sp^{9\ 29\ 77}$	P^{20}
Vaccinium myrtilloides	S	W	$D^{6\ 80}$	A^{60}	$Er^{13\ 30B}$	A^{78}	V^{80}	I $S^{31\ 56\ 70\ 80}$	Rh^{80}	$G^{71\ 80}$
Viola species	H	H	D^{T}	A^{60}	V-$A^{12B\ 30B\ 42B}$	$P^{5B\ 35B}$	U^{M}	I S^{8}	Rh^{20B}	G $P^{20B\ S}$

Trait Matrix Notes

[A] Species described by a synonym in the reference cited

[B] reference refers to another species of the same genus

[C] reference refers to the genus in general, or the species names involved were not recorded

[D] Even though Lycopods are typically infection-free as adults, the gametophyte frequently has an V-A mycorrhizal infection

[E] Dyer and Lindsay (1992) presume these species to be long lived but do not have strong direct evidence

[F] Morin and Payette (1987) and Qi and Scarratt (1997) did not observe *Trientalis borealis* in the seed bank though it was present in the vegetation, but Hiirsalmi (1969) notes that the seeds can remain dormant for years and are very difficult to germinate suggesting that the species can form long-term seed banks.

[G] Reference refers to the entire family

[H] The dispersal mechanism is inferred from the information in the reference based on the syndromes described in van der Pijl (1969)

[I] The pollination mechanism is inferred from the information in the reference based on the syndromes described in Faegri and Van der Pijl (1971)

[J] Phalanx and Guerilla strategies inferred based on the descriptions in Lovett Doust (1981) and Hutchings and Bradbury (1986)

[K] Ridley (1930) notes that most species of *Carex*, even those with habitats far from streams, have seeds that float well and appear to be well adapted for water-borne dispersal

[L] Mulligan and Munroe (1981) report no published information on mycorrhizal infection in *Prunus virginiana*, and Malloch and Malloch (1981; 1982) report that the species is only rarely infected and that the entire subfamily (Rosoideae) typically has low levels of infection

[M] There is evidence suggesting that these species may employ ant and ballistic (*Viola*) dispersal mechanisms (van der Pijl 1969), but there are no direct observations.

[N] There is evidence suggesting that this species may be vertebrate or water dispersed (van der Pijl 1969) but there are no direct observations

[O] Other species in these genera were found in the seed bank by Leckie *et al.* (2000), however this is weak evidence as their methodology was insufficient to distinguish between the transient and persistent seed banks (Baskin and Baskin 1998)

[P] This species is presumed to be in this category due to seed morphology consistent with that noted for the category by Thompson and Grime (1979).

[Q] This species does not clearly match any of the dispersal syndromes described in van der Pijl (1969), so it is classed as unspecialized.

[R] Savile (1953) notes that *Mitella* species have a splash-cup dispersal mechanism, but as this species is the only one in this community that appears to utilize this short-distance dispersal vector it was classed as unspecialized.

[S] Lamb, Stewart, and Mallik, Unpublished data

[T] Personal Observation