RIPARIAN VEGETATION PATTERNS AND LINKS WITH SURFACE WATERS IN THE BOREAL FOREST

by

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ABSTRACT

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Riparian areas in the Canadian boreal forest represent the transition zone between terrestrial and aquatic ecosystems. Factors that influence riparian vegetation communities and the associated interactions with boreal streams were reviewed. Regional and local drivers (e.g., climate and site hydrology) that affect upland boreal vegetation also operate in riparian areas. However, the proximity of riparian areas to the stream channel not only modifies some of these drivers, but it means that the stream itself becomes a driver of riparian vegetation dynamics. For example, hydrological disturbances like flooding and ice scour affect soil texture and alter successional pathways, sometimes completely denuding streambanks of vegetation. Even in riparian areas unaffected by such catastrophic disturbances, saturated soil conditions can influence riparian forest composition and nutrient cycling. Saturated soils support lower mineralization rates, therefore organic layers store relatively more carbon and nitrogen than adjoining upland soils, and primary productivity is generally lower. Saturated soils also have implications for the ability of the riparian area to "buffer" streams from surface and subsurface inputs of water and nutrients. For example, reducing conditions in riparian soils could be the sites for nitrate removal from groundwater by denitrification. Spatial variation in weather, soils, vegetation, and relief undoubtedly add to the complexity of understanding the role of riparian systems in Canada's vast boreal forest. However, the opportunity to identify patterns relating to riparian areas will assist in understanding and management of these multifaceted systems.

Among forested settings, riparian areas have been identified as having the most diverse vegetation, yet riparian communities seem to be among the least studied. The Forest Watershed and Riparian Disturbance project, a small watershed project initiated on the Boreal Plain, provided an opportunity to examine riparian diversity. The study design consisted of pre-harvest/reference, one year post-harvest, and six year post-fire data collection and included: two mature stand types (deciduous: *Populus tremuloides* and *Populus balsamifera* and coniferous: *Pinus contorta* and *Picea mariana*), three vegetation communities (riparian, transition, and interior forest) inventoried for four layers (ground vegetation (<1 m), shrubs (1 to 3 m and >3 m), and trees), and four treatments ('cut-to-shore', 30 m buffer, fire, and pre-harvest/reference sites). Three transects with plots for all vegetation layers were established for 22 sites. Species inventory was used to calculate species richness (number of individual species) which was then subject to analysis. Overall, deciduous stands were more species rich when compared to coniferous stands. Pre-harvest/reference species richness for the: (1) deciduous stands for all vegetation layers remained relatively constant for the three communities, (2) coniferous stands for ground vegetation and shrub layers decreased from riparian to interior forest communities, (3) deciduous tree layers remained relatively similar for the three communities sampled, and (4) coniferous tree layers increased from riparian to interior forest communities. Post-treatment species richness for the: (1) tree layer of both stands in transition and interior forest communities decreased one year post-harvest under cut-to-shore conditions, (2) deciduous shrub > 3 m and 1 to 3 m layers decreased one year post-harvest under cut-to-shore conditions in interior forest, and riparian and transition communities respectively, (3) tree layer of both stands under buffer conditions is maintained in interior forest communities and in transition communities of coniferous stands when compared to cut-to-shore conditions, (4) ground vegetation layer of both stands under buffer conditions is maintained in interior forest communities when compared to cut-to-shore conditions, (5) coniferous stands appear to have re-established in all layers of as well as in shrub layers of deciduous stands six years post-fire, (6) tree, tall shrub, and ground vegetation layers of coniferous communities were generally less than that found in deciduous communities six years post-fire, and (7) ground vegetation layer for both stands appeared to be uniformly well established six years post-fire.

Keywords: Boreal forest; Buffers; Disturbance; Riparian area; Specie richness, Streams; Vegetation dynamics

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CHAPTER 1: RIPARIAN AREAS IN THE CANADIAN BOREAL FOREST AND LINKAGES WITH WATER QUALITY IN STREAMS[1]

1.1 INTRODUCTION

Of the many definitions available, this review defines riparian areas in forested environments as the transition zones between the aquatic environment and the arborescent vegetation, which extends away from the channel bank or shore and includes the land and water that are associated with controlling the flux of energy and nutrients, as well as biotic interchanges (Gregory et al. 1991). Debates surrounding the definition of riparian areas are often centered on management prescriptions, the environments to consider as riparian (such as communities bordering wetlands, streams, lakes, and rivers), and the ecological functions of riparian areas (Ilhardt et al. 2000; Lee and Smyth 2003; Lee and Barker 2005). Riparian areas have been recognized as having environmental, social, and economic importance with regards to wildlife habitat, biodiversity, surface water quality, recreation, and primary resources (e.g., forestry and mining) (CCFM 1998a; Naiman et al. 1988; Twery and Hornbeck 2001; Hull et al. 2003).

Riparian areas in forested settings represent zones of ecological significance because they house diverse and dynamic biophysical habitats (Naiman et al. 1993), in part because they are exposed to disturbance events of intermediate frequency and intensity that usually prevent complete elimination of less competitive organisms (intermediate disturbance hypothesis; Hutchinson 1953). Their relationship with surface waters is reciprocal: not only do they influence streamflow and water quality, but there is strong evidence that hydrological disturbances, such as water level fluctuations, floods,

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erosion, and alluvial deposition are the primary drivers of riparian vegetation dynamics, diversity, and nutrient cycling. (Naiman and Decamps 1997; Pabst and Spies 1998). Riparian vegetation communities are also influenced by factors like precipitation, the amount and quality of runoff water from upland areas, light, air temperature, and soil conditions. Natural (e.g., wildfire, beaver activity) and human (e.g., fire suppression, harvesting, site preparation) disturbances have the potential to influence riparian area dynamics because they also alter these physical factors. For example, a riparian zone (Fig. 1.1.A.) could be exposed to higher light conditions and flooding because of tree removal due to beaver activity (Fig. 1.1.B.) or enhanced runoff from harvested upland areas (Fig. 1.1.C.). The challenge to understanding riparian vegetation ecology lies in the lack of baseline data such as riparian vegetation responses to disturbance, and the absence of clearly defined fundamental relationships such as riparian area microclimate and linkages with nutrient dynamics (Nilsson 1992). Data on riparian area form and function are essential inputs to developing qualitative and quantitative descriptions of near-shore and aquatic ecosystem response to forest disturbance.

More than three-quarters of Canada's forested land lies within the northern boreal region, between 50 and 60 degrees north latitude (NRC 2006a). This review focuses on two Canadian boreal forest ecozones: the Boreal Shield and Boreal Plain (Fig. 1.2). The Boreal Shield has thinner soils (Peters et al. 1995) and relatively more conifer-dominated terrain (NRC 2006b) than the Boreal Plain to the west (Fig. 1.2). Whereas the Boreal Shield climate is humid (annual precipitation 400 to 1600 mm), the Boreal Plain is subhumid or semi-arid (annual precipitation 300 to 625 mm) (Zoltai et al. 1998; NRC 2006b). A south to north temperature gradient exists in addition to this moisture gradient.

This is manifested by the increasing occurrence of permafrost and accumulation of organic layers at the soil surface in more northerly boreal forests (Zoltai et al. 1998; Metcalfe and Buttle 2001).

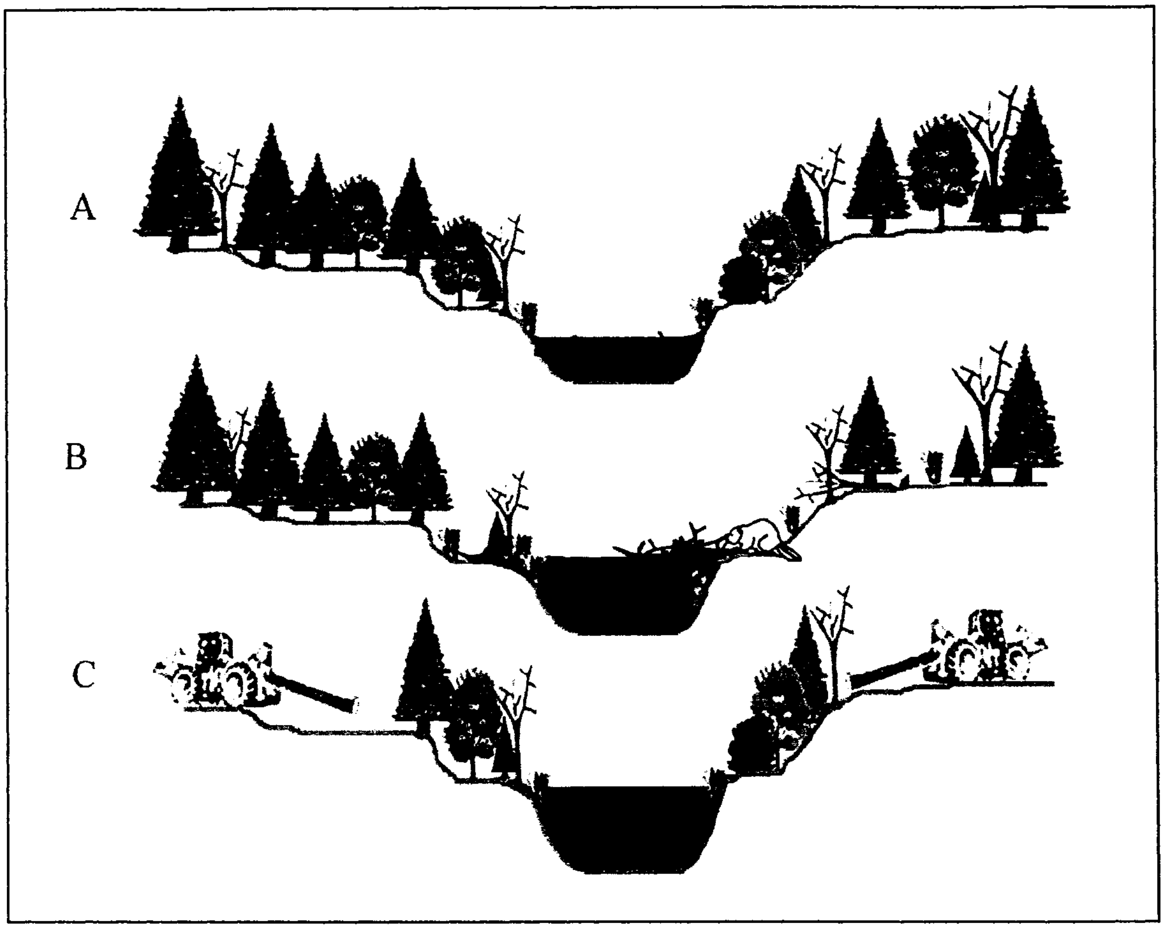

Figure 1.1. Riparian and upland factors that affect vegetation diversity and stream water quality. A, a relatively undisturbed riparian area; B, biological disturbance (e.g., beaver activity increases: water level increases, coarse woody debris increases, trees are felled); C, anthropogenic disturbance (e.g., harvesting: trees are felled, water level rises, sedimentation increases).

The Canadian boreal forest faces increased disturbance from human activities, including road construction, oil and gas exploration and extraction, hydroelectric development, mining, insect control, fire suppression, recreation, and timber harvest. For example, forestry constitutes the largest resource-based industry in Canada and approximately half of the Canadian boreal forest is accessible by roads (NRC 2006a). In addition, 25% of the freshwater surface area on earth is within Canada (CCFM 1998b), of which a significant portion (30% or 540 000 km^2) is in the boreal region (Canadian Forestry Association 2006). The elevated level of industrial activity in the boreal forest, combined with the importance of surface water resources, has heightened efforts by foresters, biologists, hydrologists, geomorphologists, and others to examine the role of riparian areas as "buffers" between watershed vegetation and receiving waters. Growing pressures to quantify environmental implications of silviculture (including: road construction, harvesting, renewal, and tending), a movement towards legislated science-based forest planning (Allen and Barnes 1985; CCFM 1998a), and issues relating to overlapping jurisdictions and cumulative impacts in managed forests (Smith et al. 2003) have accentuated the need to better document riparian functions in the Canadian boreal forest. Currently, Canadian Provincial jurisdictions have a broad range of forest retention (buffer zone) guidelines surrounding waterways (see Lee et al. (2004) for examples), which are used to regulate only those activities directly related to the wood products industry.

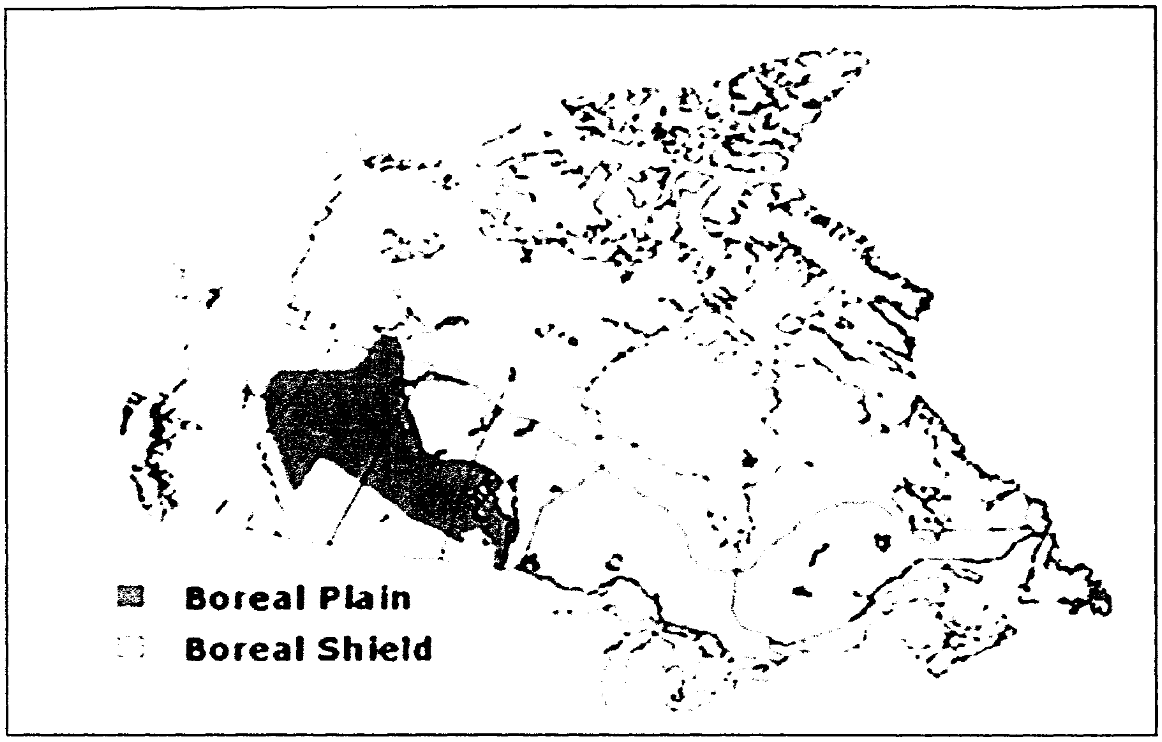

Figure 1.2. The Boreal Plain and Shield Subregions within the Canadian boreal forest.

The vegetation dynamics of riparian areas have been reviewed on a continental scale (e.g., Gregory et al. 1991; Naiman and Dècamps 1997), where different waterbody types (i.e. streams and lakes) were considered together in an attempt to reveal landscape level patterns. The importance of riparian areas in many forested systems outweighs their relatively small proportion of the land base, because their physical location means that they can function as both a hydrological link and hydrological barrier between upslope areas and the stream channel (Gregory et al. 1991; Burt 2005). This review focuses specifically on the Canadian boreal forest and the associated flowing waters because of the immediate connection they provide, relative to lakes and ponds, between upland disturbance and downstream response (e.g., Carignan and Steedman 2000; Kreutzweiser et al. 2004). The two main objectives of this review are to: (i) synthesize research related to riparian areas in the Canadian boreal forest, recognizing other sources when necessary (e.g., northern Europe) and (ii) draw attention to key gaps in riparian knowledge in the Canadian boreal forest as a basis for future research initiatives. The primary topics covered include: the role of and controls on riparian vegetation in the boreal forest (section 1.2), linkages between riparian vegetation and the aquatic (primarily stream) environment (section 1.3) and finally, the use of riparian areas as buffers to forest disturbance (section 1.4).

1.2 RIPARIAN AREAS IN THE BOREAL FOREST

Given that riparian areas represent a forest edge bordering water, riparian vegetation is influenced by factors that control upland boreal forest vegetation, as well as those related to edge effects and proximity to water. Consequently, in this section, when information specific to riparian areas is lacking, upland/inland concepts relating to riparian areas were applied. Establishment and persistence of riparian vegetation in the boreal forest is largely determined by: (i) climate – light quantity and quality, temperature, and moisture, (ii) edaphic conditions – soil conditions, in particular as they relate to saturation (texture, nutrient mineralization, pH), and (iii) natural disturbances – flooding, ice scour, beaver activity and wildfire.

1.2.1 Climatic controls on boreal riparian vegetation

On a global scale, the northern and southern boundaries of the boreal forest are defined by macroclimate factors (see Bonan and Shugart 1989), such as frost-free days and precipitation. Within boreal forest biome, a complex array of vegetation communities (ecozones) has developed based on differing climate and landscape characteristics, which include the: Boreal Plain, Boreal Shield, and Boreal Cordillera. Climatic characteristics of the: Boreal Plain are cold winters and moderately warm summers largely influenced by continental climatic conditions; Boreal Shield with the exception of the coastal margins where climate is moderated by maritime conditions, has a strong continental climate - long, cold winters and short, warm summers; Boreal Cordillera are long, cold winters with short, warm summers influenced by the Pacific Maritime conditions (CCFM 2005). Photosynthetic efficiency, which largely determines plant competitiveness and success, varies by species and is largely driven by climatic factors such as light, temperature, atmospheric and soil moisture, and ambient CO_2 concentration (e.g., Lundmark et al. 1998; Chen et al. 1999; Odasz-Albrigtsen et al. 2000; Stenberg et al. 2001). Riparian areas, nested within ecozones exhibit a unique suite of environmental conditions and add another layer of complexity to this hierarchy (Hylander et al. 2002).

Vegetation communities in the Canadian boreal forest include the following conifer tree species: white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.), jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), Engelmann spruce (*Picea engelmanni* Parry ex. Engelm.), balsam fir (*Abies balsamea* (L.) Mill.), and tamarack (*Larix laricina* (Du Roi) K. Koch). Broad-leaved trees are represented by: trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.). Common shrubs are: Labrador tea (*Ledum groenlandicum* Oeder), willow (*Salix* spp.), alder (*Alnus* spp.), and bracted honeysuckle (*Lonicera involucrata* Banks ex Spreng.). Compared to boreal forest vegetation as a whole, riparian vegetation communities appear to exhibit more spatial variability in vegetation features (e.g., density, basal area, canopy height, and vertical structure) and higher deciduous shrub and herbaceous cover (Mosley et al. 2006). However, a consistent definition cannot be applied across the boreal forest region for those plant species that constitute riparian communities. A general statement that can be made is that riparian vegetation communities in the Canadian boreal forest consist of species adapted to a wetter, more hydrologically dynamic environment than upland forests.

Light quantity and quality are critical drivers of plant competition (Ter-Mikaelian et al. 1997) and community composition (Shropshire et al. 2001). The duration of daylight and light intensity reaching the top of the forest canopy varies strongly on a daily and seasonal scale in the boreal region. In northerly latitudes, day lengths range from less than 8 hours during the winter to more than 18 hours in the summer, however maximum incoming (short wave) radiation levels are low (<1000 W m^{-2}) due to low solar elevation (Baldocchi et al. 2000). The diffuse nature of sunlight may contribute to the high light use efficiencies inferred by Still et al. (2004) for vegetation in boreal regions relative to regions at lower latitudes. Cloud cover further modifies light intensity and quality (Lieffers et al. 1999), adding another level of variability to the light regime.

Vegetation also modifies light, leading to differing light environments in the understory and canopy. As light passes through or is reflected by vegetation, light intensity decreases and the relative proportions of the various wavelengths change. Above the forest canopy, there are peaks in blue and green wavelengths (450 to 570 nm), whereas under forest cover, the peak occurs in the lower end of the infrared spectrum (Gates 1965). The structure (i.e. light interception efficiency) and function (i.e. light conversion efficiency) of leaves in full light ("sun leaves") versus shade ("shade leaves") are quite different (Kimmins 1997; Reich 1998; Stenberg et al. 2001) and one tree or shrub can exhibit leaves of both types. In general, deciduous foliage absorbs red light

(655 to 665 nm) better than coniferous foliage (Messier et al. 1989). Because of this physiological difference, as well as morphological differences between these two broad groups, light use efficiency is lower in the North American than the Eurasian boreal region, where deciduous species dominate (Still et al. 2004).

As boreal forest stands age, tree establishment, stand structure, and vegetation community composition change in response to changing light conditions (Chen and Papadiouk 2002). Pioneer plants, such as grasses, fireweed (*Epilobium angustifolium* L.), balsam poplar, and jack pine tend to be adapted to high light environments (i.e. shade intolerant), whereas later successional species, such as Labrador tea, bunchberry (*Cornus canadensis* L.), and balsam fir tend to be shade tolerant and are found under fully developed canopies. In general, understory growth is light limited after canopy closure in boreal forests (Lieffers et al. 1999). If the overstory of an established riparian area community is removed, the light environment at the ground level will change such that the next community will have to succeed under higher light conditions. Similarly, as a riparian community ages and larger shrubs or trees become established, the understory transforms to incorporate plants that can exist in a lower light environment. Understory vegetation species will differ in their response to disturbance with respect to shade tolerance levels (Harper and Macdonald 2001). For example, forest harvest improved seedling establishment and growth of shade intolerant species in a taiga forest in Canada (Bock and van Rees 2002). Seedlings and saplings that can modify their physiology and morphology in response to varying light conditions will have the best chance of survival (O'Connell and Kelty 1994). For the boreal forest, these adaptations will vary among species groups due to ontogenetic constraints (Kneeshaw et al. 2006).

Light intensity affects soil temperature. The forest floor receives more solar radiation after forest removal. In a Boreal Plain study, mineral soil temperatures in August were an average of 3°C higher in riparian clearcut sites (without site preparation) than undisturbed sites. Mineral soil moisture content was also higher at the clearcut (32%) than undisturbed (23%) sites. The linkage between forest harvest and increased light intensity can also have a direct effect on the vegetation composition of a site. For example, after clearcutting a boreal forest in northern Europe, Palviainen et al. (2005) documented a decrease in feather mosses (e.g., schreber's moss (*Pleurozium schreberi* Brid)) and stair-step moss (*Hylocomium splendens* (Hedw.) B.S. & G.). Increased light intensity and soil temperature can affect site hydrology by modifying moisture levels and can affect vegetation community composition by altering the existing microclimate.

Cool air temperatures generally limit growth in boreal forests, however, boreal riparian vegetation may be less affected than upland vegetation due to a difference in the micorclimate. On average, air temperatures remain below freezing for up to 6 months each year, and the growing season is short, less than 120 days (Baldocchi et al. 2000). Conifers in the boreal forest are not photosynthetically active in cold winters (Man and Lieffers 1997) and deciduous trees are leafless from approximately late September to May. Freezing air temperatures can damage photosystem II (the membrane protein and pigment complex that uses light energy to generate ATP) in spruce and pine under high light conditions (Lundmark and Hällgren 1987). Frozen soils also impede vegetation growth by preventing stem cambial cell division and the uptake of nutrients and carbon dioxide (Jarvis and Linder 2000). Cold soil temperatures in the boreal forest also slow soil organic matter decomposition rates, thus limiting nutrient cycling (Bonan 1990;

Gower et al. 2001) and further reducing growth potential. The organic content of the soil and distance to the stream can affect the depth of frozen soil. For example, in the boreal forest of northern Sweden, Nyberg et al. (2001) observed that the drier upland mineral soil had a deeper frost depth when compared to riparian organic soils. In addition, the fraction of soil water remaining unfrozen at temperatures well below the freezing point was much higher in the riparian organic soils (10 to15 vol.%, compared to 5 to 7 vol.% in the upland mineral soil).

Transpiration is critical for the regulation of water balance, turgor pressure, and leaf temperature. Transpiration rates are determined by the water vapour gradient between the leaf mesophyll and the atmosphere outside the leaf. Therefore, in addition to depending on leaf characteristics, transpiration rates are negatively associated with higher atmospheric moisture and positively associated with higher air temperature and soil moisture (Sen'kina 2002). Transpiration rates are generally lowest in fall and highest in mid-summer and are higher for deciduous than conifer leaves. In west-central Canadian boreal forests that were studied as part of the BOREAS project, transpiration rates measured in the field from June through September ranged from 1.3 to 4.6 mmol H_2O m^{-2} for trembling aspen leaves (Middleton et al. 1997). Among conifers, transpiration rates ranged from 0.8 to 1.4 mmol H_2O m^{-2} and from 0.5 to 1.3 mmol H_2O m^{-2} for jack pine and black spruce needles, respectively (Middleton et al. 1997). Data from the Russian taiga indicate that transpiration rates from fir and larch are higher than from pine and spruce (Sen'kina 2002). Relative to shade intolerant plants, shade tolerant plants like spruce use water more efficiently (Patterson et al. 1997) and have a narrower range in terms of transpiration changes in response to increased moisture and temperature

(Sen'kina 2002). It is reasonable to expect transpiration rates to be higher in riparian than upland forests due to edge effects and increased soil moisture because riparian areas receive water from streams, upland areas, and in some cases, groundwater (Tabacchi et al. 2000; Brooks et al. 2003). For example, water use by trees was 50% higher at the north-facing edge than in the interior of a Scots pine (*Pinus sylvestris* L.) stand in boreal Sweden (Cienciala et al. 2002)

1.2.2 Edaphic controls on riparian vegetation

Edaphic factors that affect boreal forest vegetation include soil texture, soil bulk density, soil moisture, organic matter, nutrient availability, and pH. For the riparian area, control of community composition and growth rates of individual plants is mediated through the interaction of these factors with soil saturation and concomitant reducing conditions. The importance of edaphic factors is demonstrated by research, their inclusion in the preliminary steps of site classification and the presence of an edaphic grid (usually nutrient status *vs* moisture regime) in many regionally based ecosystem classification guides (e.g., Archibald et al. 1996; Beckingham and Archibald 1996; Beckingham et al. 1996). The broad range of guides that exist reflects the spatial and temporal variation in vegetation community structure across the Canadian boreal forest.

Riparian soil profiles are subject to stream channel wandering and periodic sediment deposition after flooding events, therefore soil texture can vary among riparian sites along a stream reach and with soil depth at a given site. In general however, riparian soils such as Regosols are poorly developed (Arocena and Abley 2006) and often coarse textured (Brooks et al. 2003; BLM 2003). Soil texture has implications for saturation and oxygen conditions. Coarse-textured soils transmit water rapidly and tend to be well aerated, whereas fine-textured soils have slow transmission rates and display periodic hypoxia (BLM 2003). Riparian soils are saturated at least some of the time or at some depths; therefore riparian vegetation communities contain species that tolerate inundation, such as willow and birch. Vegetation that is tolerant of hypoxic or anoxic conditions (i.e. via aerenchyma formation, adventitious root development, or quiescence) grows where riparian soils are fine-textured (BLM 2003).

Variation in riparian vegetation, such as communities of trees, shrubs, herbs, and bryophytes on fine-grained floodplain soils (Nilsson 1999) has also been linked to soil texture via rooting ease (Jones 1983). Within the boreal forest, the rooting zone is quite shallow relative to forests farther south. More than 80% of root biomass is in the upper 30 cm of the soil, a value that is exceeded only in the tundra (Jackson et al. 1996). Reported maximum rooting depths among all terrestrial biomes is highest for trees (approx. 7 m), lowest for herbaceous plants (approx 2.4 m) and intermediate for shrubs (approx. 5 m) (Canadell et al. 1996). Given the proximity of the riparian area to the water table, rooting depth is more limited by saturated (anoxic) soils as noted above, than by soil texture directly.

Nutrient pools in riparian soils differ from upland soils. Upland soils are generally considered to have higher nutrient availability because drier and warmer conditions promote mineralization relative to downslope areas (e.g., Grant 2004). Indeed, carbon and nitrogen stores in the organic layers of riparian forest soils in central Canada were higher than in upland areas (Hazlett et al. 2005), which suggests that plant matter was accumulating. Nutrients can be translocated into the riparian area from upstream (flooding) and upland (erosion and leaching) areas. However, soil saturation in the riparian zone limits plant colonization, rooting depth, and nutrient mineralization, therefore it is probably the dominant factor responsible for observations (e.g., France et al. 1998) of lower vegetation production rates in riparian versus upland areas. The seral stages of riparian vegetation also determine the amount and structure of forest floor nutrient pools (depth and location, chemical quality, and amount of decomposition). For example, as communities move from deciduous shrub dominated to coniferous tree dominated, forest floor thickness increases until the end of the aggradation phase (Paré and Bergeron 1995). There tends to be more organic matter in the soil profile of older/more mature riparian forests when compared to younger/less mature forests (Fig. 1.3.) (Schwendenmann 2000; BLM 2003).

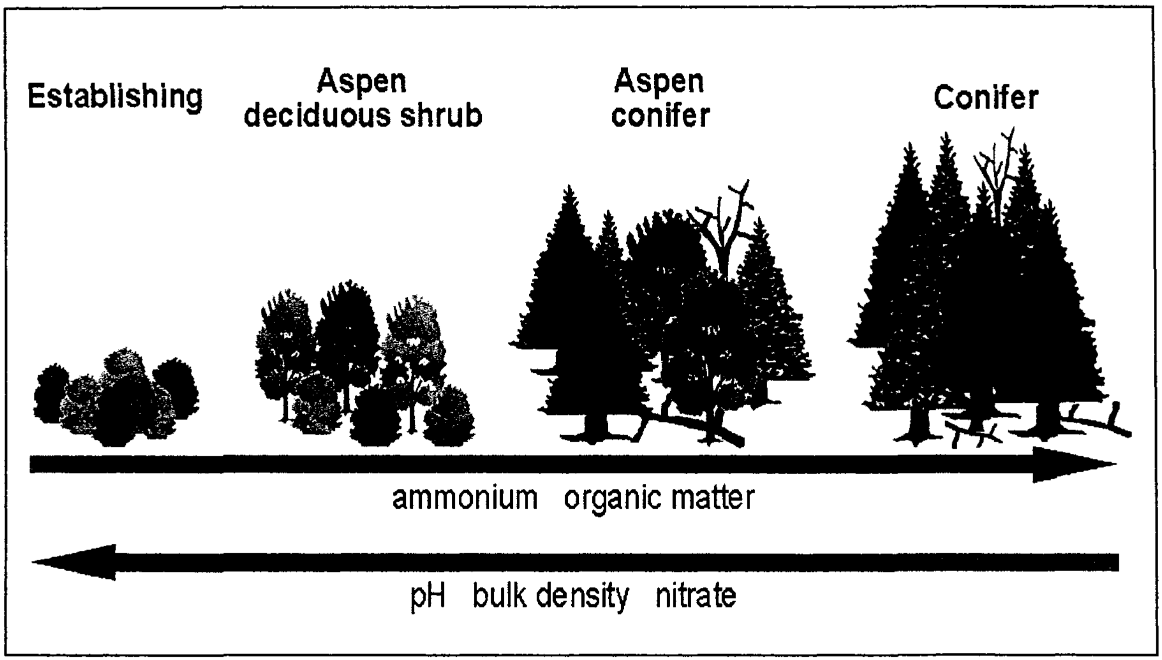

Figure 1.3. Forest seral stages and the influence of stand growth on soil ammonium, organic matter, pH, bulk density, and nitrate.

Soil pH is inversely related to the seral stage of boreal vegetation (Schwendenmann 2000) and pH also decreases as communities move from deciduous shrub dominated to conifer tree dominated (Brais et al.1995). In turn, pH affects vegetation growth through its influence on nitrification and ammonification. In general, acidic conditions are associated with lower net nitrification rates (Ste-Marie and Paré 1999) and thus lower nitrate availability. In contrast, ammonification is often stimulated by acidic conditions (Pajuste and Frey 2003), which are thus associated with higher ammonium availability (Fig. 1.3.). Several coniferous species take up ammonium preferentially over nitrate (Kronzucker et al. 1997; Min et al. 2000). In addition, some boreal trees (e.g., Scots pine, Norway spruce (*Picea abies* (L.) Karst.)), shrubs (e.g., bilberry (*Vaccinium myrtillus* L.)), and grasses (e.g., *Deschampsia flexuosa* (L.) Trin.) appear able to utilize organic forms of nitrogen (Naesholm et al. 1998) produced through nitrogen fixation (Brady and Weil 1999). A positive relationship between nitrogen fixation and forest succession rates has been observed in northern boreal stands of fire origin (Zaçkrisson et al. 2004), suggesting that as pH decreases, nitrogen fixation becomes more important.

Bulk density is generally higher in establishing vegetation communities (3 to 4 m above the channel) when compared to mature vegetation communities (6 to 8 m above the channel) (e.g., Schwendenmann 2000) (Figure 3). In addition, forest harvest has been associated with increased soil bulk density and higher soil moisture (reduced soil water deficits and lower soil moisture recharge requirements) (Cheng 1989). For example, on Boreal Plain floodplain and terrace sites that were clearcut in the winter, bulk density of the forest floor was higher (0.18 g cm^{-3}) compared to undisturbed sites (0.12 g cm^{-3}) (Schwendenmann 2000). These alterations mean that more water is available for streamflow. For example, clearcutting of lodgepole pine over 25% of a watershed was followed by an increase in annual water yield of 52% and an increase in mean daily maximum discharge of 66% during the summer (Burton 1997). Effects on peakflows are less consistent among studies, but the generalization has been made that snowmelt-derived peak flows may be higher (increased snow accumulation in cleared areas) and occur earlier (more rapid snowmelt in cleared areas) (Verry et al. 1983; Matheussen et al. 2000). This pulse of water within the stream network would undoubtedly have local and downstream effects in terms of stream biogeochemistry. Effects of higher bulk density in adjacent soils will vary for each stream channel based on disturbance type, timing, frequency, duration of exposure, and the stream morphology that existed before the pulse.

1.2.3 Natural disturbance impacts on riparian vegetation

Hydrology is the dominant natural factor shaping riparian vegetation composition and structure (Naiman and Décamps 1997). Flooding of riparian areas next to stream channels can have an immediate and dramatic impact on riparian vegetation. For example, floods were estimated to explain 72% of riparian forest structure on the Peace River in western Canada (Timoney et al. 1997). The magnitude of the impact depends upon flood magnitude, duration and frequency, as well as timing of the flood relative to the growth phase of the vegetation (Johansson and Nilsson 2002). Floods create the opportunity for new vegetation to establish because: (i) silt is deposited over existing vegetation creating a new floodplain, (ii) vegetation is uprooted to create gaps, (iii) organic matter is removed and mineral soil is exposed (large floods), (iv) unstable substrate is created, and (v) anoxic conditions can evolve (Gurnell 1997; Naiman and Décamps 1997; Gomi et al. 2002). The variability in flood frequency, duration, magnitude, and effects of floods on riparian communities are well documented in the

United States (e.g., Hupp and Osterkamp 1996; Swanson et al. 1998; Friedman and Lee 2002; Shafroth et al. 2002) and northern Europe (e.g., Johansson and Nilsson 2002) but poorly documented in Canada.

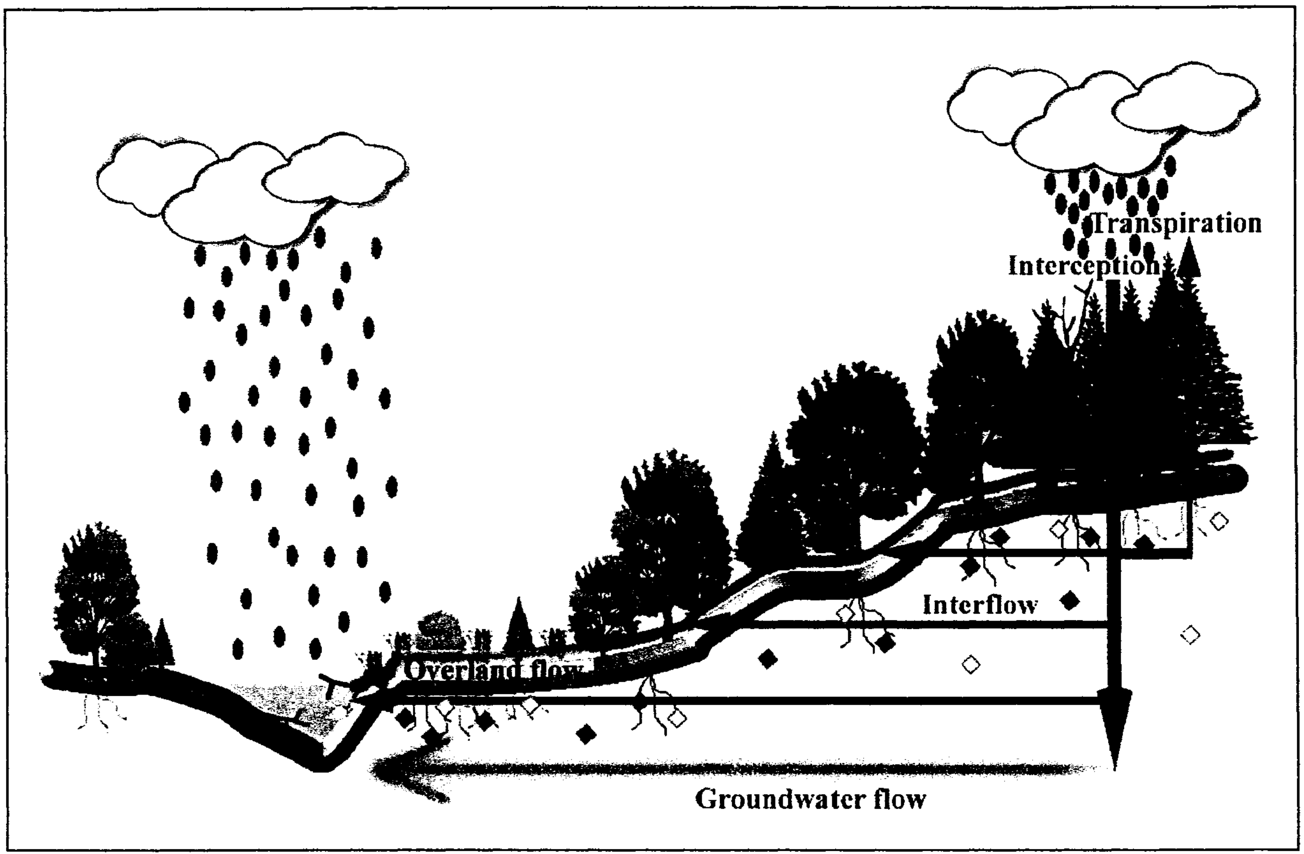

Figure 1.4. Topographical/lateral gradients of plant community composition between aquatic and terrestrial environments and linkages to water movement. Precipitation may be intercepted by vegetation or move as subsurface flow to the stream channel (blue arrows) or to the water table (indicated by the hazy blue line). Also, water flowing to the stream channel will come into contact with soil nutrients (red and yellow diamonds), especially near plant roots.

Topographic or lateral (from the stream channel to upland forest) and longitudinal (from upstream to downstream reaches) gradients in plant community composition (Fig. 1.4.) are intimately linked to the flood history of a given stream. In western Canada, flooding history is reflected in the mixture of age classes within the herb, shrub, and tree communities on the floodplains, terraces, or hillslopes immediately adjacent to stream channels. Active floodplains are usually composed of barren silt with little or no vegetation. Younger plants representing pioneer deciduous species (e.g., *Alnus* spp. and *Salix* spp.) are typically found on the first terrace 3 to 4 m above the stream channel, whereas later successional communities are found 6 to 8 m above the stream channel (Timoney et al. 1997; Schwendenmann 2000). The transition in vegetation communities from riparian to upland areas is similar in many studies, such as Nilsson (1987) and Lamb and Mallik (2003). For example, Mallik et al. (2001) observed that many boreal species either increased or decreased dramatically in abundance with distance from the stream. Graminoids and herbs presented the strongest relationship in terms of topographic/lateral gradients, increasing in mean representation as the distance (0 to 5 m) from the stream increased. Shrubs, liverworts, and mosses also increased along the topographical/lateral gradient but peaked about 3 m. Along a longitudinal gradient, plant communities resemble the upslope forest in constrained upstream reaches (often small headwater streams), where the riparian area is narrow. Moving downstream, where streams are larger and unconstrained (e.g., braided, meandering), riparian areas are wider and plant communities consist of heterogeneous patches of various successional stages. Representatives include herbs, grasses, deciduous trees, and conifers of many ages (Gregory et al. 1991).

Flooding affects riparian vegetation regeneration. Survival and growth of species such as *Betula* spp. was reduced when submerged due to flooding for about 30 days. In contrast, little influence of flood duration was observed for *Carex* spp. (Johansson and Nilsson 2002). Clearly, the tolerance of plant species to under-water submersion will affect a sites vegetation diversity. Further, degraded streambanks may be subject to a loss or change in riparian plant species (Naiman and Décamps 1997). Riparian vegetation regeneration downstream of an unstable bank may also be affected by accelerated rates of erosion, as the sediment contributed to the floodplain can be substantial. The redistribution of sediment within riparian areas can disturb established plants and limit regeneration success of certain species; however, it can also favour young and productive stages of vegetation (Nilsson and Svedmark 2002).

Physical impediments to flow are important components of the hydrological disturbance regime and can affect riparian vegetation regeneration. Coarse woody debris (CWD), beaver dams, and ice can increase movement of flood waters and sediment from the stream channel to the floodplain (Prowse and Culp 2003). CWD can also slow streamflow, create steps and pools, retain or move materials, modify stream morphology, and create habitat (Gomi et al. 2003). Slower streamflow can alter sediment loading patterns downstream, thereby affecting vegetation establishment. Beaver dams are capable of holding sufficient water and retaining deposited organic and inorganic matter (often referred to as sedimentation) (Naiman et al. 1986) therefore when a dam breaks, material held by the impoundment migrates down the channel network and can affect translocation and accumulation of debris and nutrients, as well as nutrient availability (Naiman et al. 1994). The presence of ice in a stream channel means that flooding associated with ice breakup in spring tends to be more severe than that which occurs when the channel is ice-free (Prowse and Culp 2003). Channel morphology will play a large part in determining whether physical impediments (e.g., CWD, sediment, ice) move down the stream channel or are pushed up on the bank.

Ice scour can occur in association with spring ice breakup, when moving ice is blocked by stationary ice (generally still attached to streambanks), creating ice jams that gouge the streambank and streambed (Beltaos 2000). The incidence, timing, and duration (in the order of weeks in the boreal region) of this disturbance depend on ice conditions in the channel and air temperatures in the spring. The expectation is that more "dynamic" breakup events would have a negative effect on riparian vegetation and that less intense events would have little to no effect or even enhance diversity. Dynamic ice scour events can remove riparian vegetation from streamside locations such that recolonization occurs annually, in particular at bends in the channel (Prowse 2001; Prowse and Culp 2003). In many cases, tree growth will occur only above the zone of ice action along a stream (Prowse 2001).

The American beaver (*Castor canadensis*) is ubiquitous in the Canadian boreal forest, and in particular in riparian forests. In addition to altering stream hydrology through dam building, beavers selectively cut trees, choosing poplar, aspen, and willow over fir and spruce (Pastor and Naiman 1992). As of the mid-1980s, the beaver population in North America was estimated to be 6 to 12 million animals (Naiman et al. 1986). The lifespan of a beaver can be as long as 12 years, during which time an individual can fell more than 200 trees annually (CWS and CWF 2006). By creating gaps in riparian forest, shade-intolerant, early-successional species are favoured (Pastor and Naiman 1992) (Figure 1). Therefore, beavers can have a significant impact on the landscape by altering vegetation patterns. The number of studies relating to beaver activities and landscape change is limited. A regional study in east-central Canada noted that the influence of beaver on riparian vegetation extends to be approximately 20 m from a beaver pond (Barnes and Mallik 2001). When deciduous trees comprise riparian vegetation, beaver activity may enhance water, particulate, and dissolved matter losses movement to streams because water and nutrient uptake by vegetation is reduced. Beaver management in the boreal forest has remained essentially unchanged since their reintroduction just over a half century ago, and consists of removal on an *ad hoc* basis.

As an edge environment, the riparian area may be more susceptible to windthrow. The relative impact of windthrow as a disturbance agent depends on the local wind regime, orientation of a given riparian area to prevailing winds, stream 'valley' width and slope, riparian forest density, soil depth, and the type of trees present (Steinblums et al. 1984). Tall and shallow-rooted (e.g., spruce) trees are particularly susceptible to windthrow (Burton 2002). Clearcutting experiments in sub-boreal spruce forests demonstrated that edges were associated with windthrow levels 27% (south facing edges) to 216% (north facing edges) higher than was seen in forest interiors (Burton 2002).

Wildfire frequency, size, and intensity vary according to climate and topography, within the context of human intervention (Bergeron 1991). Riparian areas may burn less often and less intensely than their upland forest counterparts, due to their proximity to the waterbreak and high soil moisture. For example, fire frequency was lower in lowland stands of black spruce and white spruce than in upland stands of jack pine and trembling aspen in the relatively dry Boreal Plain forests of western Canada (Larson 1997). Regardless, wildfire can still be a strong determinant of boreal riparian communities and was the origin of 29% of undisturbed Boreal Plain forest stands on the Peace River in western Canada (Timoney et al. 1997).

The potential exists for the relative abundance of riparian plant species to be affected by wildfire that burns only the adjacent uplands. After fire in an upland Boreal Shield forest, early successional species such as red raspberry (*Rubus idaeus* L.), which had dominated upland vegetation before fire, became more prevalent in the riparian upland transition after the burn (Lamb et al. 2003). In addition, higher light levels after upland canopy removal near this transition zone may have caused the increased abundance of some riparian species (Lamb et al. 2003). On the whole, propagule longevity, burial patterns, and response to fire of most boreal species are poorly documented (Whittle et al. 1997). In riparian areas, as in other areas, recovery rates and patterns for non-commercial species are less understood than for commercial species (Whittle et al. 1997), whether the disturbance is fire or harvesting (covered in section 1.4.).

1.3 RIPARIAN VEGETATION AND THE AQUATIC ENVIRONMENT

Numerous studies on agricultural watersheds document the influence of riparian areas on streamflow and the movement of particulates and solutes to stream channels. Due to resource limitations, studies are often constrained as to the number of variables that can be assessed. However, patterns can be derived when theory and empirical evidence from various disciplines (i.e. forestry and hydrology) are merged to detect for example, effects of forest harvesting on hydrological pathways. The review emphasizes linkages between forested riparian areas and the biogeochemistry of associated streams, including: streambank morphology and stability as they relate to channel integrity and sediment inputs, watershed runoff, nutrient concentrations in stream water, and stream microclimate.

1.3.1 Sediment inputs and streambank stability

One of the key functions ascribed to riparian zones in agricultural (e.g., Cooper et al. 1987), rangeland (e.g., Pearce et al. 1998a, 1998b), and forested settings (e.g., Clausen et al. 2000) outside the boreal forest is to trap or slow sediment being transported to the channel network in overland flow (surface runoff generated when water flows on the soil surface because it is prevented from infiltrating by impervious, frozen, or saturated soil layers) (Whigham et al. 1988; Gregory et al. 1991; Buttle 2002; Brooks et al. 2003). However, overland flow is rare when soils are unfrozen in the boreal forest because infiltration rates tend to be high relative to precipitation rates. On the Boreal Shield, soils are thin and on hillslopes, most precipitation water moves through preferential vertical flow paths in soils (e.g., dead roots) to the bedrock-soil interface and then along that shallow subsurface flow path to the stream channel (Peters et al. 1995; Hill et al. 1999). Similarly, infiltration rates tend to be high in the clay-poor surface (organic LFH and coarse-textured Ae) horizons of the Orthic Gray Luvisol soils that overlie glacial deposits on the Boreal Plain (ESWG 1996; AAC 1998). In addition, the water storage capacity of unsaturated upland soils overlying glacial deposits is high (Hinton et al. 1993; Nichols and Verry 2001). Thus, overland flow in the boreal forest is temporally restricted to periods when snowmelt or rain events occur on frozen ground or permafrost (e.g., Carey and Woo 2001; Jones and Pomeroy 2001; McEachern et al. 2006), which can constitute a significant portion of total annual runoff in mid- to high-latitude boreal forests (Metcalfe and Buttle 2001). Overland flow is spatially restricted to localized areas where soils are saturated, bedrock or other impermeable layers (including roads) are at the surface, or soils are compacted by harvesting activities or site preparation (Alcázar et al. 2002; Whitson et al. 2003).

Within this context then, the ability of boreal riparian forest vegetation to trap sediment depends upon soil type, vegetation cover, slope, accumulation of organic matter, and geographic location. Bulk density (inversely proportional to infiltration rates and, therefore, affects the capacity of soil to absorb water) is higher in early successional stages of riparian areas (Schwendenmann 2000) (Fig. 1.3). As riparian vegetation becomes more established and increases in plant abundance and species diversity, more complex rooting systems develop, increasing soil porosity and soil infiltration rates. Above ground, these changes are associated with increased physical impediments such as stems, CWD, and leaf surface, further decreasing the energy of overland flow. In addition, older seral stages that have more complex and larger plant species than younger seral stages, generally contribute larger amounts of organic matter, which absorbs and retains water. Collectively, older seral stages, more complex communities, larger vegetation, and an increase in organic matter accumulation all affect the capacity of riparian areas to buffer streams from sediment inputs.

In low relief areas of the boreal forest, sediment movement to aquatic systems from forests is not likely to be substantial, even after forest harvest (Steedman and France 2000), except where roads are located on stream crossings. In a high-retention buffer watershed (removal of all merchantable timber >30 cm diameter at breast height (DBH) within 20 m of the stream), post-harvest suspended sediment levels were observed to return to or become lower than pre-harvest predicted levels within three years or less (Macdonald et al. 2003b). By comparison, a low-retention buffer watershed (removal of all merchantable timber, >15 cm DBH for pine and 20 cm DBH for spruce within 20 m of the stream), suspended sediment levels did not return to pre-harvest predicted levels (Macdonald et al. 2003b). Ancillary activities associated with forest harvesting, such as road construction, can be a significant contributor of sediment loading to streams. For example, culvert installation and bridge construction on separate small boreal headwater streams in eastern Canada were followed by increased sediment loading compared to reference streams (Clarke and Scruton 1997).

Another mechanism by which riparian vegetation affects sediment loads to streams is stabilization of stream banks. Vegetation maintains bank stability and lessens erosion, especially during flood events (Nilsson and Svedmark 2002), by the combined effect of low pore pressure in streambank soils (from high evapotranspiration rates) and root strength (Brooks et al. 2003). Riparian root studies are scarce, particularly for Canada's boreal forest. Riparian root biomass studies in the northeastern United States documented that in the top 30 cm of an undisturbed site, the average root biomass was 1330 g m^{-2} (Kiley and Schneider 2005). Upland forests have significantly lower amounts of root biomass. For example, in a mature northern hardwood forest of the United States, root biomass was only 471 g m^{-2}. If riparian root systems are damaged, streambanks may be subject to a loss of soil or a loss of or change in riparian plants species (Naiman and Décamps 1997). Riparian areas downstream of an unstable bank can experience accelerated rates of sediment deposition, because the sediment contributed to the floodplain can be substantial (Timoney et al. 1997; Jeffries et al. 2003). The redistribution of sediment within riparian areas may disturb established plants and limit regeneration success of certain species; however, it may also favour young and productive stages of vegetation (Nilsson and Svedmark 2002).

1.3.2 Streamflow and runoff

Water enters the riparian zone from the stream channel, and from upland areas as: overland flow (rare on unfrozen soils in the boreal, as noted in section 1.3.1); interflow, generally defined as event water movement through shallow subsurface soil layers, and separated from the groundwater by an impervious layer of some sort; and groundwater flow (Fig. 1.4). Interflow is thought to be the most important flow path in the boreal forest, but groundwater can also be an important constituent of soil moisture in the riparian area because of its the lowland position (Brooks et al. 2003). In most field studies at the watershed scale, runoff is measured at the stream channel, therefore it represents an integration of overland flow, interflow, groundwater flow, and direct interception of precipitation by the stream channel (Brooks et al. 2003) (Fig. 1.4). In this section, the term runoff applies to this watershed-scale integrated response, unless otherwise noted.

Riparian vegetation has the potential to physically influence streamflow (e.g., direct interaction with overbank flow, induction of turbulence by roots), overland flow, and interflow (e.g., alteration of infiltration rates by riparian litter and root macropores) (Tabacchi et al. 2000). Within the saturated sediment that forms the boundary between the riparian area and stream, the hyporheic zone (see section 1.3.3), there also exists the potential for physical and chemical exchanges between water from upland areas and stream water. These local scale processes occurring between riparian vegetation, riparian soils, and runoff water combine to affect water movement at the regional or landscape scale (Tabacchi et al. 2000; Burt 2005).

In undisturbed boreal forests, water movement to the riparian zone from upland areas is determined in part by air temperature and precipitation patterns on both annual and seasonal scales. During periods when soil moisture is high (e.g., during spring melt and storm events), the riparian zone is linked to upland areas. Conversely, when soil moisture is low, the riparian area is hydrologically decoupled from upland areas (Burt 2005). On a regional scale then, water sources to the riparian area may be intermittent in semi-arid Boreal Plain forests, unlike more humid Boreal Shield forests. On a local scale, runoff can be variable among years within a given watershed, as well as among watersheds within a given year. For example, runoff varied by factors of 5 and 6 within large (>1000 km^2) Boreal Shield and Boreal Plain watersheds, respectively, between 1980 and 2004 (Environment Canada 2005). Similarly, during one year, runoff varied by up to 5 times among 9 first to third order Boreal Plain watersheds covering an area of only 230 km^2 (Prepas unpubl. data).

In spring through fall, relatively more rain arrives at the stream channel if it falls prior to leaf out or after leaf off, since interception and uptake of water by deciduous vegetation is lower. In winter, snowfall not only determines the potential spring runoff, but in combination with air temperature and soil moisture conditions prior to the winter, it determines the depth of soil frost. In general, soil frost inhibits infiltration, wetter soils are more impermeable than dry soils when frozen (less porosity), and organic soils have shallower frost depths than mineral soils. Spring rains falling on frozen soils rapidly generate overland flow. From 25 to 100% of precipitation became runoff (measured at the stream channel) when litter and upper soil organic horizons in Boreal Shield forests were frozen (Jones and Pomeroy 2001).

Wetlands cover approximately 46% of the Boreal Plain and 18% of the Boreal Shield (CCWS 2003) and their distribution within watersheds contributes to the temporal and spatial runoff variation noted above. Wetland cover within relatively undisturbed Boreal Plain watersheds has been positively associated with total runoff for three open-water seasons (May through October) (Prepas et al. 2006, unpubl. data). This suggests that wetlands accumulate and temporarily store spring melt waters, then release them (less water losses to evapotranspiration) to the stream channel during the open-water season. Alternatively (or additionally), wetland cover may simply be an indication of water table conditions in a watershed, with high groundwater discharge rates in watersheds with high wetland cover. Water movement through peatland-dominated watersheds is more complex. Peatlands, defined in Canada as wetland areas where at least 40 cm of peat accumulates (CSSC 1978), gain importance on the landscape in more northern boreal forests, where poorly drained soils - and sometimes discontinuous or continuous permafrost - and a cool climate slow decomposition rates and promote peat development (Zoltai et al. 1998). Their variable water storage ability, unpredictable flow paths, and the occurrence of permafrost complicate measuring water movement through peatland systems (McEachern et al. 2006).

Within the context of this myriad of factors that vary spatially and temporally and interact in a variety of ways, some broad generalizations can be made about boreal riparian vegetation in terms of its interaction with water moving from upland areas to streams. 1) Soils and litter layers in riparian areas are wet relative to upland areas year-round, therefore the capacity for riparian soils and litter to directly absorb runoff is limited. 2) Uptake of runoff water by riparian vegetation and soils is higher when antecedent soil moisture is low. 3) Soil in more mature riparian forests has a higher water holding capacity than less mature forests, in part due to more organic matter in the soil profile (Schwendenmann 2000; BLM 2003). 4) Moist soils, combined with edge effects, means transpiration may be a significant route for water loss from the riparian zone during the growing season. 5) The importance of spring melt as a component of total annual runoff in many boreal forest watersheds means that a significant portion of runoff water moves through the riparian zone before vegetation is active.

1.3.3 Nutrient concentrations

Tree growth in boreal riparian zones may be more limited by nutrients than water because saturated soils are associated with lower mineralization rates (Grant 2004). However, it has not been conclusively demonstrated that riparian areas in the boreal forest consistently reduce nutrient concentrations in water moving to stream channels. Detection of patterns is made difficult by the suite of processes that add spatial and temporal complexity to nutrient dynamics in riparian areas such as atmospheric deposition, fixation, sorption/desorption, transformation, uptake, leaching, and erosion. In the Canadian boreal forest, concentrations of nitrogen and phosphorus in streams and receiving waters have been the focus of a limited number of watershed studies and will be addressed here. On a regional scale, water quality concerns center on inorganic nitrogen on the Boreal Shield where thin soils overlay bedrock (Peters et al. 1995) and harvesting could lead to higher levels of mineralization and leaching (Simard et al. 2001; Hazlett et al. 2006). Water quality concerns in forests on the Boreal Plain center on erosion of soils derived from phosphorus-rich sedimentary parent materials (Prepas et al. 2003; Burke et al. 2005).

Partitioning of water between surface and subsurface flowpaths is an important determinant of nutrient movement to streams. Water that reaches the stream channel by overland flow on frozen soils is relatively dilute, having had little to no interaction with organic and mineral soils (Metcalfe and Buttle 2001). Particularly in northern boreal watersheds, timing of snow melt and spring rain events relative to soil thaw (active layer development) determines how much of the snow water and spring rain infiltrates into soils (Metcalfe and Buttle 2001). Slope angle was proposed to be a key feature to regulate partitioning of runoff between surface and subsurface flow paths on unfrozen soils in Boreal Shield watersheds, with lower slope angles (more saturation) supporting relatively more overland flow (D'arcy and Carignan 1997). On the other hand, on the relatively low-relief Boreal Plain, soil texture influences flow path partitioning, because wetland formation is linked with fine soils in lowland areas. In wetlands, most water is routed through shallow subsurface flow paths through organic layers (Schiff et al. 1998). Water leaving wetlands is in equilibrium with organic soil water, particularly in peatlands, because "old" water in the peatland is displaced by event water in a process termed piston flow (McEachern et al. 2006).

Nutrients in water moving through the rooting zone in the riparian area are taken up (plant and microbial uptake, sorption), released (desorption, decomposition), and transformed (primarily microbial cycling of nitrogen). Water that is not taken up by plants moves through the soil as interflow or groundwater flow (Fig. 1.4). Alterations to water chemistry in riparian soils depend upon conditions along the flow path (e.g., reduction-oxidation potential, presence of electron acceptors and substrates, microbial community composition) and residence time in the riparian zone. As noted by Burt (2005) for denitrification, when water residence time is short, there is little opportunity for the process to occur before water enters the stream channel; yet when water residence time is long, denitrification occurs but the water volume entering the channel is low and stream chemistry is not greatly affected.

At the riparian groundwater-stream interface (hyporheic zone), mixing involves at least two hydrological pathways: groundwater inputs to the channel (gaining streams) and channel inputs to groundwater (losing streams) (Hill 1990; Dahm et al. 1998). This hydraulic gradient is highly dynamic, particularly in semi-arid forests, with the net water movement to the stream channel possible at one time and the net water movement to the hyporheic zone possible at another time. Similarly, water may enter the hyporheic zone from the stream in one portion of a stream bank and leave it farther downstream (Brooks et al. 2003). The hyporheic zone is also an active site for chemical and biological transformations that yield water that is low in dissolved oxygen, organic matter and available nutrients relative to stream water (Brooks et al. 2003).

Gross primary productivity in the boreal is limited by several factors including length of growing season, average annual temperature, soil moisture and nutrient availability. Most nitrogen in forest ecosystems is derived from nitrogen fixation by symbiotic and free-living microorganisms and stored in soils, primarily (~80%) as organic nitrogen that is not accessible by plants (Fenn et al. 1998). On the Boreal Shield, riparian forest stands had higher nitrogen stores in forest floor material and lower nitrogen stores in mineral soils than upland stands (Hazlett et al. 2005). Nitrogen cycling in soils is affected by plant uptake and litterfall, and factors that influence the composition and activity of microbial populations, namely soil temperature, moisture, and reduction-oxidation potential (Pinay et al. 2002). Ammonium usually comprises much more of the inorganic (bioavailable) nitrogen fraction than nitrate in soils of closed boreal forests (Brais et al. 1995, Smith et al. 2000) (Figure 3). Nitrification, the biochemical oxidation of ammonium to nitrate mediated largely by autotrophic bacteria, is more likely to occur under aerobic conditions, as would be common in well-drained upland soils. This process, however, is limited by ammonium (substrate), carbon, and oxygen. Nitrate is more mobile in solution than ammonium and is therefore the form of inorganic nitrogen most lost through leaching from the soil system (Munson and Timmer 1995). Whenever nitrate exists in excess of plant or microbial demand, there is the potential for leaching in ground and surface waters.

Denitrification in organic soils and riparian groundwater is viewed as the main pathway by which nitrate from runoff in settings where nitrogenous fertilizers are used is removed from riparian areas (Hefting et al. 2005). It is the biologically mediated reduction of nitrate to gaseous nitrogen (molecular nitrogen or as an oxide of nitrogen). Conditions in riparian soils and groundwater that support denitrification are saturation/anaerobiosis and high carbon availability. There is the potential for this process to be more important in deciduous- than conifer-dominated areas, because it is inhibited by low pH (Dhondt et al. 2002). Available nitrate is rarely found in the soil of mature, closed forests therefore the raw material for denitrification is unavailable. However, significant denitrification has been measured after stand disturbances, such as harvesting (Martin 1985), suggesting that excess nitrate is readily available. In sites where upland disturbance results in conditions that favour nitrification over denitrification (that is, drier rather than wetter soils), excess nitrate may be transported towards streams. Under these conditions, riparian areas gain importance as zones of denitrification. In addition, riparian areas may buffer streams in areas where high atmospheric nitrogen deposition rates (e.g., up to 13 kg ha^{-1} y^{-1} in some areas on the Boreal Shield; Jeffries 1995) could cause nitrogen saturation.

A second pathway by which gaseous nitrogen might be generated in riparian areas is anaerobic ammonium oxidation (anammox), a process that involves combining ammonium and nitrite, the latter which may have been generated by denitrification (Burgin and Hamilton 2007). Among freshwater systems, this process has only been documented in Lake Tanganyika, where it was estimated to contribute up to 13% of the gaseous nitrogen produced (which would previously have been attributed to denitrification) (Schubert et al. 2006). It is plausible that anammox could occur at or near aerobic-anaerobic interfaces in boreal soils, wetlands, hyporheic zones, and streambeds, because the bacteria that mediate anammox appear to have a low optimal temperature (Jetten 2001) and the process requires the presence of both nitrate and ammonium (Burgin and Hamilton 2007). However, anammox is inhibited where there are high concentrations of labile carbon (Jetten et al. 1998), a common condition in these environments. Ammanox remains to be studied as a pathway for nitrogen transformation in boreal forest riparian areas.

The length of contact time between water and soil along hydrologic pathways influences the biotransformation of nitrogen in runoff. Increasing contact between water and soil or sediment increases nitrogen retention and microbial transformations, provided the flow intercepts roots and microorganisms (Pinay et al. 2002). For example, on the Boreal Shield, Hazlett and Foster (2002) observed depletion of ammonium and H^+ ions as forest floor leachate moved downslope and into mineral soils. The process of nutrient exchange between water to sediment also occurs in stream channels. In a comparative study that observed headwater streams from biomes throughout North America, Peterson et al. (2001) reported that the most rapid uptake and transformation of inorganic nitrogen occurred in the smallest streams. Small streams have shallow depths and narrow surface to volume ratios, characteristics that increase the contact between water and sediment, and favour nitrogen uptake and removal processes (e.g., denitrification). It is reasonable to hypothesize however, that headwaters will have threshold values for nutrient retention above which changes to water quality and perhaps habitat quality might be expected. The derivation of threshold values based on site-specific information and the length of contact between water and soil may provide an important indicator of disturbance and recovery.

More so than nitrogen, phosphorus is often the growth-limiting nutrient in fresh waters. Saturated and potentially anoxic conditions in riparian soils and groundwater are key to phosphorus dynamics, because they mediate at least three processes. First, gleying tends to occur in saturated soils if iron or manganese is present in conjunction with other conditions (e.g., carbon and specific microbial populations). Gleying associated with reduction can lower the concentration of H^+ ions, therefore soil pH may be elevated under anaerobic conditions. Elevated pH changes the solubility and concentration of various metal (aluminum, iron) and non-metal species (calcium, potassium, magnesium) (Stumm and Morgan 1996). At neutral to basic pH, phosphorus will bind to calcium to form insoluble calcium phosphates, hydroxyapatites, and apatites. Conversely, iron and aluminum phosphate become more soluble with increasing pH. Second, the water table in the riparian area is dynamic, and changes in moisture and oxygen conditions that damage or kill fine roots (Joslin et al. 2000) and microbial populations (Sylvia et al. 1999) can result in the release of a pulse of organic acids. Short-chained organic acids (e.g., citrate, salicylate) accelerate phosphorus dissolution rates in soil via direct ligand exchange or complexation of ions (like calcium) bound to P (Jones 1998; Hinsinger

2001). Third, evidence from Boreal Plain lakes indicates that phosphorus is released from calcium and magnesium complexes in sediment under reducing conditions (Burley et al. 2001). Solution chemistry, which requires many inputs (including pH, total carbon and nutrient contents), has benefited from modelling to predict chemical speciation under the given conditions (e.g., Sposito and Mattigold 1980). Most work on solution chemistry has been done in microcosms under sterile lab conditions and it remains to be seen if theoretical predictive tools for solution chemistry can be effectively transferred to field situations.

In Boreal Plain forests, particulate phosphorus loading to streams during storm events was attributed to erosion of phosphorus-rich soils in the watershed and streambed (Prepas et al. 2003; Burke et al. 2005). Retention of particulate phosphorus by the riparian area in this setting would be directly related to sediment retention as discussed above. Shallow soils in Boreal Plain forests were sources of dissolved phosphorus under high water table conditions that saturated organic layers (Evans et al. 2000). The riparian area acted as a source of dissolved phosphorus to surface waters when the water table was high (Evans et al. 2000).

1.3.4 Stream microclimate

The influence of riparian vegetation on stream water temperatures has been well documented (e.g., Johnson and Jones 2000, MacDonald et al. 2003a; Story et al. 2003). Riparian vegetation can: (i) intercept solar radiation before it reaches the water surface and (ii) determine the means and rates of heat and water entry into, and release from, the stream environment (Poole and Berman 2001). Shading has been recognized as a contributor to maintenance of water quality (Norris 1993). Shade provides thermal protection to stream water and dissolved oxygen concentrations decrease as water temperatures increase, all else remaining equal. Conditions that reduce dissolved oxygen concentrations have implications for the ability of a stream to assimilate organic wastes without excessive oxygen depletion (Norris 1993), and the distribution and composition of species within the system (Bjornsson et al. 2001). Therefore shade has the potential to influence stream biogeochemistry appreciably. Depending on baseline water temperatures and extent of riparian vegetation, routing of water by riparian vegetation can also be important to maintaining water temperature at optimal levels.

Riparian communities and aspect also exert strong control over the microclimate of streams (Naiman and Décamps 1997; Macdonald et al. 2003a); thus vegetation within riparian areas, aspect, and the microclimates of streams are linked. For example, in the western boreal forest, Macdonald et al. (2003a) observed an increase in stream temperatures following the removal of much of the riparian vegetation. Summer mean weekly maximum temperatures increased by 4°C after harvesting, particularly in a stream with a southerly aspect, where maximum temperatures increased by nearly 6°C.

In terms of tolerance to temperature fluctuations, fish have been studied more intensively than other aquatic organisms. If a fish enters water where temperatures exceed the upper or lower limits of habitability for that species (while also considering size and sex) then that fish could die (Bjornsson et al. 2001; Davies and Bromage 2002). Fish have been used as "indicators" of stream health, but have limited usefulness as indicators in small headwater streams with little downstream connectivity, because they are usually absent. Temperature tolerances of alternate indicator organisms (e.g., macroinvertebrates, periphyton) (Hylander et al. 2002) are not as well documented as those of boreal fish species.

Studies of invertebrate and algal interactions with riparian vegetation are often confounded by two important variables, water temperature and organic inputs, which are difficult to consider separately. A positive relationship has been observed between increased amounts of solar radiation and increased algal and invertebrate community diversity and abundance (Liljaniemi et al. 2002; Kiffney et al. 2003; Melody and Richardson 2004). In some cases, this was accompanied by an increase in inorganic matter trapped by filamentous periphyton, which were dominant in areas where there was no riparian vegetation (i.e. more light) (Kiffney et al. 2003). Price et al. (2003) demonstrated that intermittent and perennial streams in old growth sites housed more algal biomass than streams with associated riparian vegetation in younger seral stages, even though the streams with the older trees had more cover (i.e. less light).

1.4 RIPARIAN VEGETATION AS BUFFERS TO FOREST DISTURBANCE

Riparian buffers around lakes, streams, and ponds have been legislated in Canada to mitigate impacts of harvesting on receiving waters. Riparian buffers are also known as: retention buffers, buffer strips, buffer zones, vegetated buffers, forested buffers, and corridors. The many definitions imply that buffers are multifunctional. For example, "vegetated buffers" are intended to interrupt the flow of surface and subsurface waters and associated substances (Norris 1993). "Riparian corridors" are linear landscape elements that provide movement between habitat patches (Rosenberg et al. 1997). Debate continues in terms of whether vegetated buffer strips *per se* or specific widths of buffer strips play a consistent role with respect to visible wildlife such as mammals and birds (Darveau et al. 1998, 2001). Whereas the concept of riparian buffers has been met with little resistance, the details of application remain contentious (Buttle 2002). The range of Provincial buffer zone guidelines in Canada reflects uncertainties surrounding variation in the amount of protection needed for different biogeophysical conditions, the ability of buffers to reduce a response within a disturbed system, and the scientific basis for present practices.

Currently, there is no universally applied context in which to classify boreal streams on the landscape, and thus to project disturbance responses. In the Foothills of the Rocky Mountains in western Canada, the ROSGEN Stream Classification system has been applied (Rosgen 1994; McCleary and Bambrick 2003). However, the process of linking harvest practices around stream channels with the ROSGEN or other rigorous stream classification systems has yet to be developed for Canadian ecoregions. Accurate databases relating to stream type and location on the landscape are essential components of classification systems. Yet the mapping of small streams in forested areas is generally inadequate in Canada (Moore and Richardson 2003). For example, in the eastern Canadian province of Newfoundland, streams must appear on 1:50 000 topographic maps to require a vegetated buffer (Curry et al. 2002). Small streams are often under closed canopies and thus are hidden from satellite or aerial imaging equipment (Naiman and Décamps 1997; Moore and Richardson 2003). Aerial photography captures small streams more effectively if implemented before leaf-out in the spring or after leaf senescence in the fall, when canopy coverage is minimal. In addition, new technologies, such as lidar, have the potential to increase the capacity to map small streams (Reutebuch et al. 2003). Ground truthing with well-trained field staff in managed forested units is probably the best method of acquiring field information with regards to small streams (see Gomi et al. 2002). Nonetheless, uncertainties remain regarding how these streams should be treated once mapped on an industrial landscape.

To date, there is scattered evidence that buffers act as semi-permeable filters for substances carried by moving water. On most landscapes, dissolved and suspended ion concentrations are influenced by land use (e.g., forestry, oil and gas, mining, and agriculture), climate, and tectonic activity (Naiman and Décamps 1997). Distinct initiatives have been documented in the Canadian boreal forest focused on lakes and changes brought about by forest harvesting on the Boreal Shield (i.e. Carignan et al. 2000; Lamontagne et al. 2000; Steedman 2000) and Boreal Plain (i.e. Prepas et al. 2001). In these studies, forest removal influenced the dissolved fraction of nutrients and other ions in receiving lake waters. For example, phosphorus, potassium, chloride, total organic nitrogen, and dissolved organic carbon (DOC) concentrations are all documented to increase following forest harvesting (Carignan et al. 2000; Steedman 2000). In addition, potassium and chloride export rates were positively related to the proportion of the area cut and DOC and total phosphorus export rates were directly related to the drainage ratio (drainage area divided by lake area) (Lamontagne et al. 2000; Carignan and Steedman 2000). Clearly, the amount harvested and drainage ratio within a watershed plays important roles in determining water quality in receiving waters after harvest. The drainage ratio for streams (drainage area divided by stream area) will be larger in comparison to that of lakes, and therefore it can be expected that streams will be magnified in their responses to harvesting with respect to increasing nutrient and ion concentration. Studies that quantify the linkages between headwaters and downstream waters are essential to understanding the role of buffer strips.

The concept of varying the width of the undisturbed riparian area relative to watershed and stream features is gaining acceptance as a means to optimize the effectiveness of the riparian buffer. The riparian vegetation community composition is one such feature that can be incorporated into buffer width optimization. Allochthonous litter inputs ranging from CWD to fine particulate matter differ in amount and quality between deciduous and coniferous riparian forests. The shift in dominant species in the riparian vegetation community, which will take place over different distances for different landform types, may have implications for aquatic organisms, particularly in heterotrophic headwater streams. In addition, the amount of CWD produced differs among seral stages. A "U-shaped" temporal trend with respect to CWD volume is often observed in forested systems. For example, in the western boreal, the volume of CWD was relatively low to intermediate in a 36 year old stand (32 m^3 ha^{-1}), lowest in a 58 year old stand (15 m^3 ha^{-1}), and highest in an 80 year old stand (78 m^3 ha^{-1}) (Sturtevant et al. 1997). Therefore, different buffer widths may be acceptable for different seral stages depending on management objectives and variables involved. Further, in northern Ontario on the Boreal Shield, mature stands harvested with varying buffer widths (30 to 300 m) within the last five years were observed to vary by 34 to 62% in CWD inputs (Kreutzweiser et al. 2005). Understanding baseline conditions and CWD inputs under natural conditions for various forest types would help in identifying appropriate buffer widths for specific stand types within specific seral stages. A second feature to consider with regards to variable buffer strip width is topography. Topography exerts control over wind speed, and therefore has an effect on CWD input distance to the stream. Topography and the width of the riparian area are determinants of the amount of wind throw within the context of forest composition and age at a site (Ruel et al. 2001).

Soil type in the riparian area can also be considered in buffer width guidelines. Relatively wet soils can be associated with low mineralization rates and nutrient availability and anoxia, which limit rooting depth and influence vegetation presence. As a result, the ability of boreal riparian areas to retain sediment, nutrients, and runoff may be limited in very wet areas. Flowing waters in granitic channels or those subject to periodic ice scour may lack vegetation from the high water mark to the zone colonized by trees. Effective buffer strips should encompass vegetated areas and their implementation should not assume vegetation begins at streamside. Further, soils that hold more water at field capacity, have relatively high organic content, and are fine textured, will likely respond more negatively to disturbance than those that hold less water when exposed to the same intensity and duration of precipitation (Archibald et al.1997). For example, forest harvesting sometimes results in soil compaction and increased soil bulk density, reducing soil water holding capacity (McNabb et al. 2001; Whitson et al. 2003). As a result, a site's existing water pathways (Whitson et al. 2005) and soil water content (Elliott et al. 1998) can be affected. The response of soil texture and structure to forest harvesting has been well studied for upland boreal stands (e.g., McNabb et al. 2001; Startsev and McNabb 2001; Bock and van Rees 2002) compared to riparian areas.

Riparian buffer strips may moderate water temperatures with respect to both surface and subsurface water supplies via shading and water uptake following clearcutting. During post-harvest periods in west-central Canada, Story et al. (2003)

observed that riparian buffer strips appeared to partially achieve the objective of shading a stream, however, other factors such as groundwater inputs may contribute to altered water temperatures in small streams fed by shallow groundwater. Groundwater inputs can be responsible for either decreased or increased stream water temperatures (Curry et al. 2002). Groundwater temperature fluxes have been linked to elevated water tables after clearcutting and therefore, subsurface water that has more opportunity for solar heating and snowpack insulation may aid in increasing stream water temperatures.

1.5 CONCLUSIONS

Riparian areas in the Canadian boreal forest are characterized by features that require careful consideration if riparian buffers and the governing legislation are to be effective at protecting flowing waters from upland disturbance. Overall, riparian vegetation studies in Canada's boreal forest are regional and do not appear to encompass intersite variation, which could stifle landscape integration of riparian areas within forest management plans. However, impacts of site disturbance can be site-specific, therefore implementing a national database or a simplified national look-up table describing the different watershed conditions and their responses to disturbances would be valuable to scientists and land managers alike. A national database housing information on changes in riparian or upland forest vegetation with and without disturbance, which incorporates elements of landscape variation with integrated resource management, would be informative for developing a science-based approach available for forest planners. Database elements could include: stream morphology, stream order, local topography, aspect, major soil and geological classifications, stream bed type (e.g., cobble, gravel, sand), role of organic (e.g., CWD) and inorganic inputs, plant species present, stand age, and past disturbances.

CHAPTER 2: EFFECTS OF FOREST HARVEST AND FIRE ON BOREAL PLAIN RIPARIAN, TRANSITION, AND INTERIOR FOREST VEGETATION COMMUNITIES

2.1 INTRODUCTION

Among forested settings, riparian areas have been identified as having the most diverse vegetation (Naiman et al. 1993). Riparian areas have also been recognized as zones of importance with regards to wildlife habitat and surface water quality (Naiman et al. 1988; Twery and Hornbeck 2001). Yet, riparian communities seem to be among the least studied (Luke et al. 2007). Documentation of natural and harvest influenced landscape patterns that specifically include riparian zones will extend the data base on vegetation patterns. The Riparian Vegetation Study (RVS) reported here provides information on species richness in three linked forest community types (riparian, transition and Interior), before and after canopy removal (harvesting and fire) in mature boreal deciduous and coniferous stands in the Swan Hills of Alberta.

In many operational forest activities, including mapping and management, the smallest unit is the stand. From an ecological point of view however, stand designations (e.g. coniferous or deciduous) are coarse and they mask the horizontal and vertical structure within. Within each stand, communities (e.g., riparian, transition, or interior forest) are distinguishable and within each community, vegetation layers (e.g. ground vegetation, low and tall shrubs, sub-canopy, canopy and super-canopy trees) exist. Each combination of stand, community and layer is likely to have a distinct species richness range (Harper and MacDonald 2001). Many jurisdictions are adopting forest classification systems that incorporate more characteristics than simply dominant tree species (e.g. Sims et al. 1990, Nesby 1997) because of the influence of these characteristics (e.g. ground cover, soil origin, depth and moisture status) on stand dynamics. In Ontario, each major region has its own specific series of silviculture manuals based on that region's ecosite classification system. Response to disturbance is also expected to vary based on species present. For example, under cut-to-shore conditions, ground vegetation under a coniferous canopy is expected to respond differently than that under a deciduous canopy because the change in light quantity and quality after harvest would be far greater for the former than for the latter. The vertical and horizontal stratification of relatively coarse stand classes to include vegetation layers and distinct patterns in vegetation cover as the distance from the watercourse increases allows for the identification of vegetation gradients, which help to describe the forested systems monitored. In this study, baseline information will be used to evaluate changes following disturbance.

The disturbance history of a site is also important to consider when interpreting species presence and abundance (Denslow 1980). Communities occupying riparian areas are prone to flooding and ice scour events, whereas those further away from the stream, such as transition or interior forest, are more likely to be exposed to fire, windthrow or harvesting (Luke et al. 2007). Most Canadian jurisdictions have adopted a "natural disturbance emulation" approach to forest management. Unfortunately, there are few data documenting natural or disturbed riparian community composition. transition zones between upland and riparian areas in Canadian forests are generally managed by leaving linear strips of forest vegetation called buffers (Lee et al. 2004). In the second year of the RVS, clearcut harvesting with and without buffers were established and monitored in three of the project watersheds. The RVS provided the opportunity to capture before and after measurements of species richness. As such, these data will contribute to the information base on natural and disturbed riparian community composition.

Wildfire has largely led to the formation of a temporally and spatially dynamic forest mosaic on the Boreal Plain of Alberta (Bergeron et al. 2002; Timoney et al. 2003). In the absence of anthropogenic disturbance, forests on reasonably well drained soils are characterized by pure and mixed stands of *Populus tremuloides*, *Pinus contorta*, *Pinus banksiana*, and *Picea glauca*. There is a noticeable shift in the *Pinus* spp. when moving from east to west on the Boreal Plain. *Pinus banksiana* generally extends from the eastern border of the Boreal Plain to central Alberta (longitude 113° W). *Pinus contorta* generally begins at this point and extends throughout the western portion of the Boreal Plain (Critchfield 1966). The RVS includes only *Pinus contorta*. Stands located in wetter areas on the Boreal Plain are characterized by *Picea mariana*, *Larix laricina*, *Populus balsamifera*, and *Betula papyrifera*. Hence, landscape characteristics such as slope and drainage favour the establishment of different tree species, which impact the composition of the vegetation layers below.

The system of allocating large tracts of forest land to private companies through Forest Management Agreements (FMA's) began in the mid-1900's in the province of Alberta. Alberta FMA's vary in size from just over 58 000 km^2 (Alberta-Pacific Forest Products Incorporated) to just under 600 km^2 (Vanderwell Contractor's Ltd.) (Sustainable Resource and Development 2006). Due to the relatively young nature of the Alberta forest industry, the opportunity to capture baseline data related to forest harvesting may be greater than in other provinces. On the same land base increased fire suppression, consistent with the increasing value of natural resources (merchantable timber and oil and gas), has also occurred (Thompson et al. 1998). This shift from fire-driven to industrially managed ecosystems may lead to changes in community structure that could influence wildlife habitat and water quality. Baseline data are necessary to assess vegetation responses to disturbance among different stand classes and various stand components.

The Forest Watershed and Riparian Disturbance (FORWARD) project, a small watershed project on the Boreal Plain (Smith et al. 2003), provided an opportunity to examine boreal vegetation in and near riparian areas under conditions of harvesting, fire and no disturbance. The objectives of the study were to: (1) inventory the species in riparian (R), transition (T), and interior forest (IF) communities of mature deciduous and coniferous stands, (2) quantify post-treatment effects of forest harvesting and fire on species richness, and (3) quantify differences between communities and vegetation layers.

The following hypotheses were tested:

(1) for the ground vegetation (GV) and shrub layers, species richness in R communities will be higher than in T or IF communities,

(2) for the tree layer, species richness will be higher in IF communities than in R or T communities, (Note: Hypotheses 1 and 2 will be considered both a. before and b. after disturbance.),

(3) clearcut harvesting reduces species richness in all communities and stand classes and cut-to-shore (CTS) harvesting moreso than harvesting with a 30 m buffer (buffer), and

(4) post-fire species richness

i. follows the same patterns identified in hypotheses 1 and 2,

ii. will be affected by pre-disturbance stand class and

iii. will differ from that in undisturbed stands.

2.2 METHODS

2.2.1 Study location and design

The Riparian Vegetation Study (RVS) is located in the Swan Hills of Alberta on Crown Land managed by Millar Western Forest Products Ltd. (MWFP) and Blue Ridge Lumber Inc. (Fig. 2.1). The study was carried out over two years (2003, 2004). The range of conditions included reference (no disturbance during the study), pre- and one year post-harvest and six years post-fire. Harvest was either 1) clearcut CTS (as operationally feasible) or 2) clearcut with buffer. Harvest, fire, and reference conditions were dispersed among 9 small watersheds (approx. 400 ha each). Due to landscape variation within the study area, neither treatments nor stand classes were equally represented in the sampling design (Table 2.1). Species richness data were collected in three distinct communities: R (within 5 m of the stream edge); T (5 to 25 m from the stream edge); and IF (15.5 to 30 m of the stream edge) in mature coniferous (primarily >70% lodgepole pine) and deciduous (>70% trembling aspen) stands. Each community was stratified into four layers - GV, low shrubs (LS) (1 to 3m), tall shrubs (TS) (>3 m) and trees (> 1 m) (Table 2.2).

Table 2.1. Mature stands (60 to 80 years since disturbance) inventoried in 2003 and 2004.

Stand	Treatment	Number of Sites
Deciduous[a]	Reference	3[c]
	Buffer	1
	Cut-to-shore	2
	Fire	1[d]
Coniferous[b]	Reference	5[c]
	Buffer	2
	Cut-to-shore	4
	Fire	4[d]
Total Sites		22

[a] >70% trembling aspen (*Populus tremuloides*), >90% when combined with balsam poplar (*Populus balsamifera*)

[b] >70% lodgepole pine (*Pinus contorta*), primarily black spruce (*Picea mariana*) in the understory

[c] all treatment data from 2003 uncut and 2004 reference stands were used as pre-treatment/reference data in statistical analysis

[d] fire data were collected in 2004

Table 2.2. Summary of the vegetation inventory, 2003 and 2004.

Component of Inventory	*N*	Summary Notes
Sites	22	19 stands, 3 sampled from 2 aspects[1]
Transects	66	3 per site
Vegetation Layers		
Ground vegetation (< 1 m)	396	2 m^2
Low Shrub (1-3 m)	198	20 m^2
Tall Shrub (>3 m)	198	20 m^2
Tree	198	60 m^2
Total	990	

[1] Aspects were separated by 180 degrees

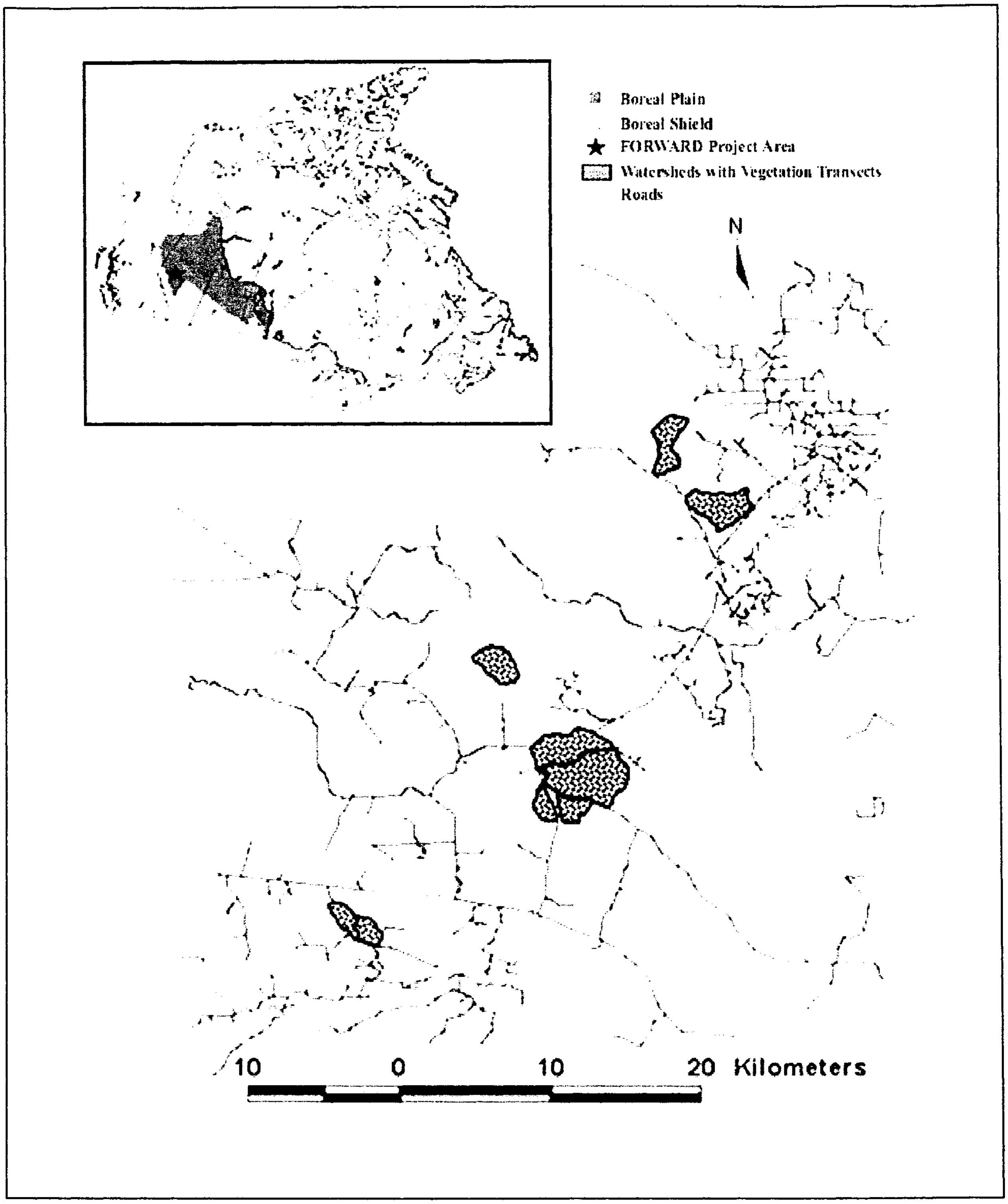

Figure 2.1. Project location, watersheds with vegetation transects, and the Boreal Shield and Plain subregions within the Canadian boreal forest.

2.2.2 Site identification

Stands used for the study were classified using the Alberta Vegetation Inventory (Nesby 1997), identified by aerial photographs and digital maps made available by MWFP and Blueridge Lumber Inc., and confirmed through ground truthing. It took approximately two months to identify and locate the 22 stands used (Table 2.2). Inventories were carried out during June and July of 2003 and 2004 along each transect. The inventory included: species identification, ecosite classification (Beckingham and Archibald 1996), topography, photographs (cardinal directions, up and down) from each plot center, and universal transverse mercator (UTM) co-ordinates. Number of species (species richness) was the variable used in the statistical and graphical (bar graph) analyses presented here.

2.2.3 Transect and plot centre establishment

With the exception of the fire stands, all stands were inventoried in the summer of 2003 to obtain pre-disturbance data. In the summer of 2004, following winter harvest, the stands were re-inventoried and fire stands were added. At this time, the fire stands were six years old.

The starting point (directly adjacent to the stream) of each transect was randomly chosen. If anthropogenic disturbances (*i.e.,* road, well site, seismic line, etc.) were encountered, another point was selected. Each transect was identified, marked, and UTM coordinates were obtained with a Garmin eTrex Legend global positioning system. A 30 m (level distance) transect was established on the azimuth running perpendicular to the stream. The first plot centre was always placed 2.5 m from stream edge to ensure the riparian vegetation was described. Subsequent plot centres were located based on the occurrence of vegetation changes (*i.e.,* there was a shift in species composition) and captured only the vegetation within the defined community. The final plot centre, together with all associated sub-plots, fell within the interior forest community. Fig 2.2 illustrates a typical transect.

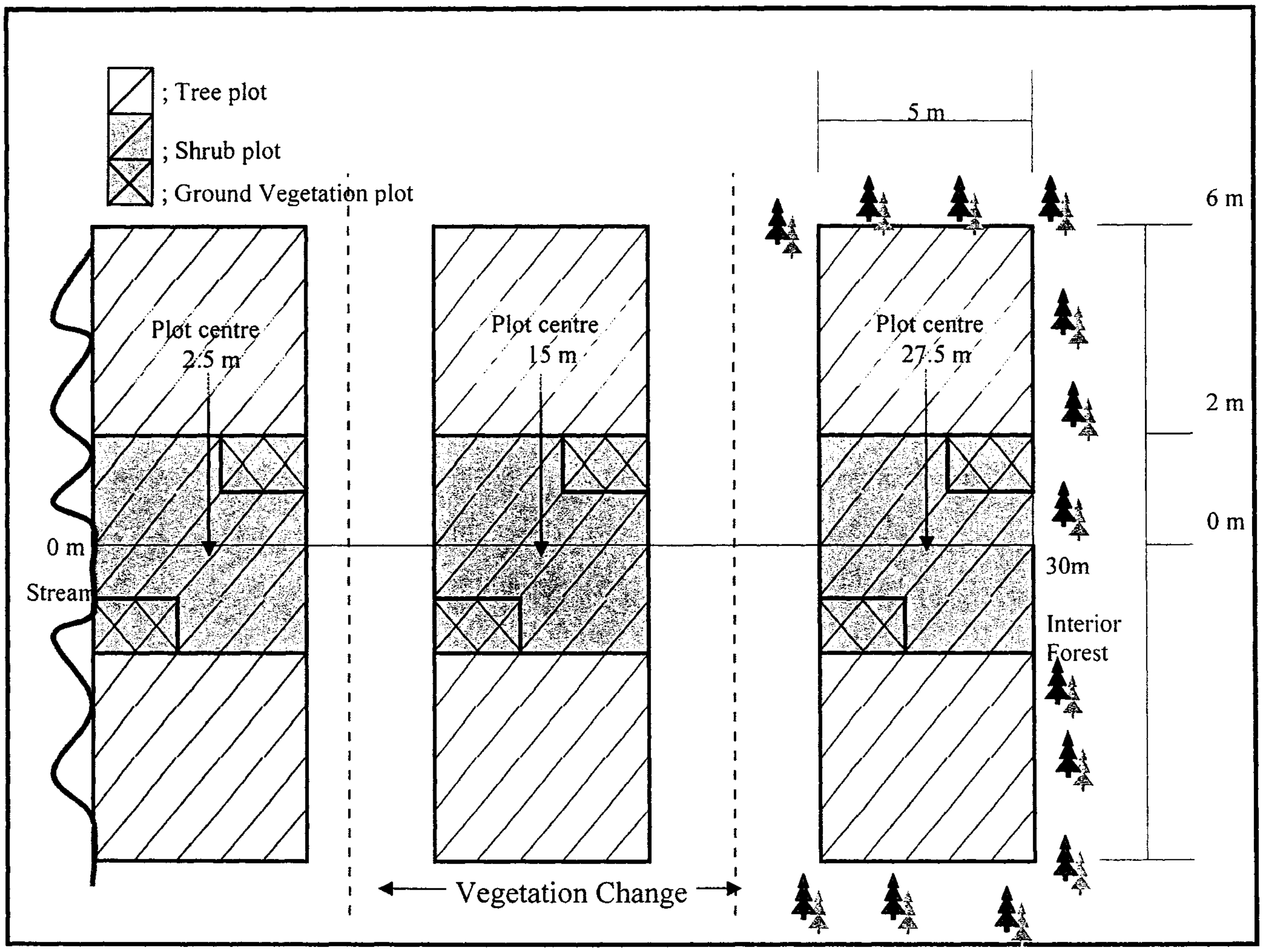

Figure 2.2. Transect diagram illustrating plot layout: six ground vegetation, three shrub (1 to 3 m and >3 m), and three tree plots.

2.2.4 Vegetation plot establishment and inventory

For each community along the transect, two 1 x 2 m sub-plots for GV, one 5 x 4 m sub-plot for sampling low and tall shrubs and one 5 x 12 m plot for sampling trees were established. GV included all plants below one metre: herbs, woody and non-woody perennials, grasses, mosses, lichens, and trees. Shrubs were stratified by height; LS (1 to 3 m) and TS (> 3 m), and were identified following Beckingham et al. (1996). Trees included any tree species taller than one metre and were identified following Beckingham et al. (1996). Almost 1000 plots and sub-plots were established over the course of two years (Table 2.2).

GV were generally identified to species, however, some were only identified to genus. These included *Carex* and *Vaccinium*; the mosses, *Polytrichum, Sphagnum,* and *Dicranum;* and the lichens, *Cladonia, Cladina* and *Peltigera.* All other lichens were classed simply as "lichen". With the exception of *Equisetum scirpoides* Michaux, *Equisetum* spp. were also identified only to genus. In the shrub strata, all willows, with the exception of blueberry willow (*Salix myrtillifolia* Anderss.), were identified as *Salix* spp.. All other shrubs were identified to species and average heights were determined. In the tree strata, all trees, with the exception of *Abies balsamea* and *Abies lasiocarpa*, were identified to species. The two firs were classified as *Abies* spp.

In addition, all transects were line mapped and included site information such as slope, aspect, percent bare ground/rock/standing water, and evidence of fire (scars, charcoal).

2.2.5 Analyses

Species richness is defined as the number of species present (Magurran 1988) and is the measure used in this thesis. Prior to testing my initial hypotheses (these are also hypotheses), I evaluated whether there were non-treatment differences in the reference stands between the two study years (2003, 2004). Differences would suggest that factors other than disturbance affected species presence. In order to capture the widest range of natural variation, I included all the 2003 (or pre-treatment) inventories from the stands scheduled for harvest as well as the identified reference stands. This resulted in an unbalanced two-way ANOVA design. The data were stand level averages for each community and layer therein. The linear model is shown in Eq. 1 and the Estimated Mean Squares in Table 2.3a. Scheffé's post-hoc tests were then used to dissect the community*year interaction and identify differences, if any, between years one and two data related to specific communities. If there were no significant interaction effects, the data for both years within each uncut community (riparian, transition, or interior forest) could be combined for use in subsequent tests.

$$Y_{ijk} = \mu + Yr_i + Cmy_j + Yr*Cmy_{ij} + \varepsilon_{(ij)k} \qquad \text{Eq. 1}$$

where:

Y_{ijk} = species richness of the $_k$th replicate of the $_j$th community in the $_i$th year

μ = the overall mean

Yr_i = the fixed effect of the $_i$th of 2 levels (2003 and 2004) of year

Cmy_j = the fixed effect of the $_j$th of 3 levels (riparian, transition, and interior forest) of community

$Yr*Cmy_{ij}$ = the fixed interaction effect of the $_i$th level of Yr with the $_j$th level of Cmy

$\varepsilon_{(ij)k}$ = the random effect of the $_k$th experimental unit within the $_{ij}$th treatment combination. The $\varepsilon_{(ij)k}$ are assumed to be IID N(0, σ^2).

Hypothesis 1 and 2 (comparison of species richness across the three communities before and after disturbance): Based on the year 1 data only, ANOVA was used to determine if stand class or community were sources of variation in any of the vegetation layers. Data for the combined 2003 uncut and 2003/2004 reference inventories were used to test for differences in the absence of disturbance while data from 2004 inventories of harvested stands was used to test for differences following disturbance. However, because community is nested in stand class, we did not have sufficient data to test their interaction or to complete typical post-hoc tests for differences between group means (see Eq. 2 and EMS Table 2.3b). Subsequently, *t*-tests (Snedecor and Cochrane 1989) were used to evaluate differences between communities within a stand class (e.g., coniferous riparian *vs* coniferous transition, coniferous riparian *vs* coniferous interior forest and coniferous transition *vs* coniferous interior forest).

$$Y_{ijk} = \mu + \text{Stand}_i + \text{Cmy}_{(i)j} + \varepsilon_{(ij)k} \qquad \text{Eq. 2}$$

where:

Y_{ijk} = species richness of the $_k{}^{th}$ replicate of the $_j{}^{th}$ community in the $_i{}^{th}$ stand

μ = the overall mean

Stand_i = the fixed effect of the $_i{}^{th}$ of 2 levels (deciduous and coniferous) of stand

Cmy_j = the fixed effect of the $_j{}^{th}$ of 3 levels (riparian, transition, and interior forest) of the community nested within stand

$\varepsilon_{(ij)k}$ = the random effect of the $_k{}^{th}$ experimental unit within the $_{ij}{}^{th}$ treatment combination. The $\varepsilon_{(ij)k}$ are assumed to be IID $N(0, \sigma^2)$.

Table 2.3 Estimated Mean Squares (EMS) tables. Vegetation layers (ground vegetation, low shrub, tall shrub and trees) and stand class (deciduous and coniferous) were tested independently. In this balanced example, there are 5 replications (or stands). The actual number of observations varied with stand class. Main factors include year (Yr: 2003 and 2004), community (Cmy: riparian, transition, interior forest) and stand (coniferous and deciduous).

a. Two-way ANOVA of reference stand data based on Eq. 1.
Main factors are year and community.

Source	*df*	F 2^a i	F 3^a J	R 5^a K	EMS	F-ratio
Yr_i	1	0	3	5	$\sigma^2 + 15\,\Phi\,\text{Yr}$	MS(Yr)/MS(E)
Cmy_j	2	2	0	5	$\sigma^2 + 10\,\Phi\,\text{Cmy}$	MS(Cmy)/MS(E)
Yr*Cmy_{ij}	2	0	0	5	$\sigma^2 + 10\,\Phi\,\text{Yr*Cmy}$	MS(Yr*Cmy)/MS(E)
$\varepsilon_{(ij)k}$	24	1	1	1	σ^2	

b. Nested ANOVA based on Eq. 2. Main factors are stand and community.

Source	*df*	F 2^a I	F 3^a j	R 5^a K	EMS	F-ratio
Stand_i	1	0	3	5	$\sigma^2 + 15\,\Phi\,\text{Stand}$	MS(Stand)/MS(E)
$\text{Cmy}_{(i)j}$	4	2	0	5	$\sigma^2 + 10\,\Phi\,\text{Cmy}$	MS(Cmy)/MS(E)
$\varepsilon_{(ij)k}$	69	1	1	1	σ^2	

[a] the number of levels relating to the factor

Hypothesis 3 (method of harvesting will affect species richness): Although a logical outcome of overstory removal is that community richness would change, this assumption was tested. As the communities were nested within stand type, I used *t*-tests to identify differences a. between reference and harvested communities and b. between harvest methods for each community. These comparisons are made for each vegetation layer separately.

Hypothesis 4 (effect of fire on species richness): *t*-tests were again used to evaluate differences between communities associated with the different stand classes (e.g. coniferous riparian *vs* deciduous riparian, coniferous transition *vs* deciduous transition, and coniferous Interior *vs* deciduous Interior). This approach allowed for different sample sizes in the groups. For all four hypotheses, *t*-tests were done manually with Excel as a calculator.

2.3 RESULTS

2.3.1 Community composition

Species found in the GV, LS, TS, and tree layers of both deciduous and coniferous stands were typical for the Boreal Plain. Although GV and tree species differed between the two stand classes, shrub layers were very similar. With the exception of *Lonicera involucrata* and *Vibernum edule* in the LS layer, common species found in both shrub layers for both stand classes were similar for all three communities and consisted of *Salix* spp., *Alnus tenufolia*, and *Alnus crispa*.

Common tree species in deciduous stands in all communities were *Populus tremuloides*, *Populus balsamifera*, and *Betula papyrifera*. Common species in the GV layers for: (1) R communities included *Equisetum* spp., and *Rubus* spp., (2) T communities were *Cornus canadensis,* and *Vaccinium* spp., and (3) IF communities were *Pleurozium schreberi* and *Cornus canadensis*. *Calamagrostis canadensis* was common in all three communities.

Common tree species in coniferous stands in all communities were *Picea mariana, Pinus contorta, and Populus tremuloides*. Common species in the GV layers for: (1) R communities were *Calamagrostis canadensis* and *Equisetum* spp. and (2) T and IF communities were *Ptilium crista-castrensis* and *Cornus canadensis*. *Pleurozium schreberi* was common in all three communities.

2.3.2 Annual differences in the reference stands

As discussed in section 2.2.5, I wished to learn if there were non-treatment differences in species richness between 2003 and 2004 in each community. In the deciduous stands, neither main effect (year, community) nor their interaction was a source of variation for any vegetation layer. For all layers of coniferous stands, the year*community interaction was insignificant hence there were no statistical differences between the 2003/2004 inventories of the three communities. However, both year and community as main effects were significant. The main effect of community for GV, LS and TS is dealt with under Hypothesis 1. The main effect of year in the GV layer likely reflects annual micro-climatic differences in the R (Δ 4 species) and T (Δ 2 species) communities. Although transects were measured at about the same time each year, differences in temperature and precipitation do occur and can affect species presence and coverage. These factors are explored in the Discussion (section 2.4). To ensure the representation of natural variation in uncut stands and increase sample size used in subsequent comparisons, 2003 and 2004 reference data for each community were pooled for all layers.

Table 2.4. a. ANOVA *p*-values and b. Scheffé's Post-hoc test comparing 2003 and 2004 species richness in the riparian, transition and interior forest communities of the uncut coniferous and deciduous stand classes. **Bolded** values are significant.

a. ANOVA Stand	Source of Variation	*df*	Ground Vegetation	Low Shrubs	Tall Shrubs	Tree
Deciduous	Year	1	0.55	0.57	0.15	0.42
	Community	2	0.72	0.84	0.54	0.22
	Year*Cmy	2	0.69	0.99	0.98	0.58
	Error	21				
Coniferous	Year	1	**0.03**	0.83	0.24	0.38
	Community	2	**<0.001**	**<0.001**	**<0.001**	0.09
	Year*Cmy	2	0.48	0.94	0.82	0.55
	Error	42				

b. Scheffé's Post-hoc test results for both stand classes (deciduous and coniferous) and all vegetation layers (ground vegetation (GV), lower shrubs (LS), taller shrubs (TS), and trees) and communities.

			Community					
Stand	Layer	Year	Riparian		Transition		Interior Forest	
			Mean	SE	Mean	SE	Mean	SE
Deciduous	GV	2003	18.9	1.6	17.3	1.3	17.8	1.3
		2004	18.4	0.6	17.9	1.3	20.2	2.7
		Overall	18.7	1.1	18.3	1.2	18.3	1.3
	LS	2003	1.7	0.3	1.6	0.2	1.5	0.3
		2004	1.9	0.4	1.8	0.4	1.7	0.7
		Overall	1.8	0.2	1.6	0.2	1.6	0.3
	TS	2003	1.1	0.2	0.9	0.2	0.7	0.2
		2004	1.3	0.3	1.2	0.1	1.1	0.6
		Overall	1.1	0.2	1.0	0.1	0.9	0.2
	Tree	2003	2.3	0.2	2.0	0.3	2.0	0.4
		2004	2.3	0.0	1.9	0.6	1.3	0.4
		Overall	2.3	0.1	2.0	0.2	1.8	0.3
Coniferous	GV	2003	15.4	1.3	13.5	0.7	11.4	0.8
		2004	19.7	2.0	15.4	2.2	12.5	1.6
		Overall	**16.7a**	1.2	**14.1b**	0.8	**11.8b**	0.7
	LS	2003	1.6	0.2	0.5	0.1	0.2	0.1
		2004	1.6	0.2	0.6	0.6	0.2	0.4
		Overall	**1.6a**	0.2	**0.5b**	0.1	**0.2b**	0.1
	TS	2003	0.8	0.2	0.3	0.1	0.1	0.0
		2004	1.3	0.2	0.6	0.2	0.1	0.1
		Overall	**1.0a**	0.1	**0.4b**	0.1	**0.1c**	0.0
	Tree	2003	2.2	0.3	2.7	0.3	3.2	0.3
		2004	2.9	0.3	2.6	0.3	3.5	0.5
		Overall	2.4	0.3	2.7	0.2	3.3	0.3

Different letters indicate significant differences at $p < 0.05$

2.3.3 Hypothesis 1a: For the ground vegetation and shrub layers in the absence of disturbance, there will be higher species richness in riparian communities than in transition and interior forest communities regardless of stand class.

The nested ANOVA identified both stand and community as sources of variation for the GV, LS and TS layers; deciduous stands had more species in each layer than did coniferous stands. Mean richness values (dark bars in Figures 2.3 to 2.5) for GV ranged from 11.8 ± 0.7 to 16.7 ± 1.2 (mean ± standard error) while those for the LS and TS were almost always less than 1.5 (± 0.5 or less). In the GV, LS and TS layers of deciduous stands, prior to disturbance, species richness in R communities was not detectably higher than in T and IF communities (Part A, Table 2.5). In contrast, in GV layers of coniferous stands, species richness in R communities was higher (16.7 ± 1.2) than in T (14.1 ± 0.8; $p < 0.001$) and IF (11.8 ± 0.7; $p < 0.001$) communities. The GV layer in T communities was also more species rich than that of the IF communities ($p < 0.001$) highlighting a gradient of decreasing richness with distance from the stream edge. Likewise, in undisturbed LS and TS layers of coniferous stands, species richness in R communities was higher (1.6 ± 0.2 and 1.0 ± 0.1) than in T (0.5 ± 0.1 and 0.4 ± 0.1; $p < 0.001$) and IF communities (0.2 ± 0.1 and 0.1 ± 0.0; $p < 0.001$). The T communities in the TS layer were also more species rich than the IF communities ($p < 0.01$) thus repeating the gradient noted in the GV layers. The hypothesis is therefore supported with respect to coniferous stands but not deciduous stands in the absence of disturbance.

Table 2.5. Comparison of mean species richness between A. Pre-harvest/reference communities and B. Post-harvest communities in deciduous and coniferous stands. Different letters indicate significant differences at $p < 0.05$.

Stand	A. Pre-harvest/Reference[1]			Treatment	B. Post-harvest[2]		
	Riparian	Transition	Forest		Riparian	Transition	Forest
i. Ground Vegetation							
Deciduous	18.7	18.3	18.3	Buffer	**21.3a**	**21.0a**	**14.8b**
				Cut-to-Shore	**23.0a**	**17.5b**	**16.7b**
Coniferous	**16.7a**	**14.1b**	**11.8c**	Buffer	**11.8a, b**	**14.3b**	**11.3a**
				Cut-to-Shore	**18.0a**	**11.9b**	**7.2c**
ii. Low Shrub							
Deciduous	1.8	1.6	1.6	Buffer	0.0	0.3	0.3
				Cut-to-Shore	2.0	0.8	0.5
Coniferous	**1.6a**	**0.5b**	**0.2b**	Buffer	**1.0a**	**0.2b**	**0.0b**
				Cut-to-Shore	**1.0a**	**0.4a, b**	**0.0b**
iii. Tall Shrub							
Deciduous	1.1	1.0	0.9	Buffer	0.0	0.0	0.3
				Cut-to-Shore	**1.5a**	**0.7a, b**	**0.2b**
Coniferous	**1.0a**	**0.4b**	**0.1c**	Buffer	0.5	0.2	0.0
				Cut-to-Shore	**0.9a**	**0.2b**	**0.0b**
iv. Tree							
Deciduous	2.3	2.0	1.8	Buffer	3.3	1.3	2.0
				Cut-to-Shore	**2.3a**	**1.2a**	**0.0b**
Coniferous	**2.4a**	**2.7a**	**3.3b**	Buffer	2.2	2.0	2.8
				Cut-to-Shore	1.4	0.8	1.2

[1] means include all pre-harvest and 2003/2004 reference data, [2] one year post-harvest.

2.3.4 Hypothesis 1b: For the ground vegetation and shrub layers after harvest disturbance, there will be higher species richness in riparian communities than in transition and interior forest communities regardless of stand class.

This section compares each of the three communities (R, T, IF) after clearcut harvest with either CTS or buffer treatments in both the coniferous and deciduous stands. Mean species richness after harvest varied from 7.2 ± 1.2 (coniferous, IF communities, CTS) to 23.0 ± 2.3 (deciduous, R communities, CTS) in the GV layer but was less than one in the LS and TS layers for all but one community (deciduous, R communities, CTS). The general species richness pattern of R>T>IF communities holds for both stand classes, both harvest methods and all three layers with three exceptions (deciduous, R communities, buffer and coniferous, R communities, buffer). In the deciduous communities however, the mean species richness values in the shrub layers are either 0.3 or 0.0 and not distinguishable.

In the GV layer, species richness in R communities exceeded that of the IF with the exception of the coniferous buffer noted above. In this case, species richness in the GV layer was highest in the T communities (14.3 ± 2.2) but only significantly so in comparison to the IF communities (11.3 ± 0.8). In both stand classes, differences between R and T and T and IF communities were inconsistent occurring in both stand classes. The coniferous CTS treatment was the only combination where all three means differed and the gradient was the same as pre-harvest.

In the LS layer of the deciduous stands, species richness did not differ between communities. However, in coniferous stands, both buffer and CTS resulted in no (i.e. 0 species) shrub species in IF communities, less than 0.5 species in the T communities and only 1 species in the R communities Differences between R and IF communities were detectable. In the TS layer and for both stands, species richness was higher in the CTS treatment than in the buffer and differences between R and IF communities were identified.

Similar to the data from undisturbed stands, the pattern of species richness decreasing with distance from the stream edge continued to hold after disturbance. Some variation associated with both stand class and harvest method was evident.

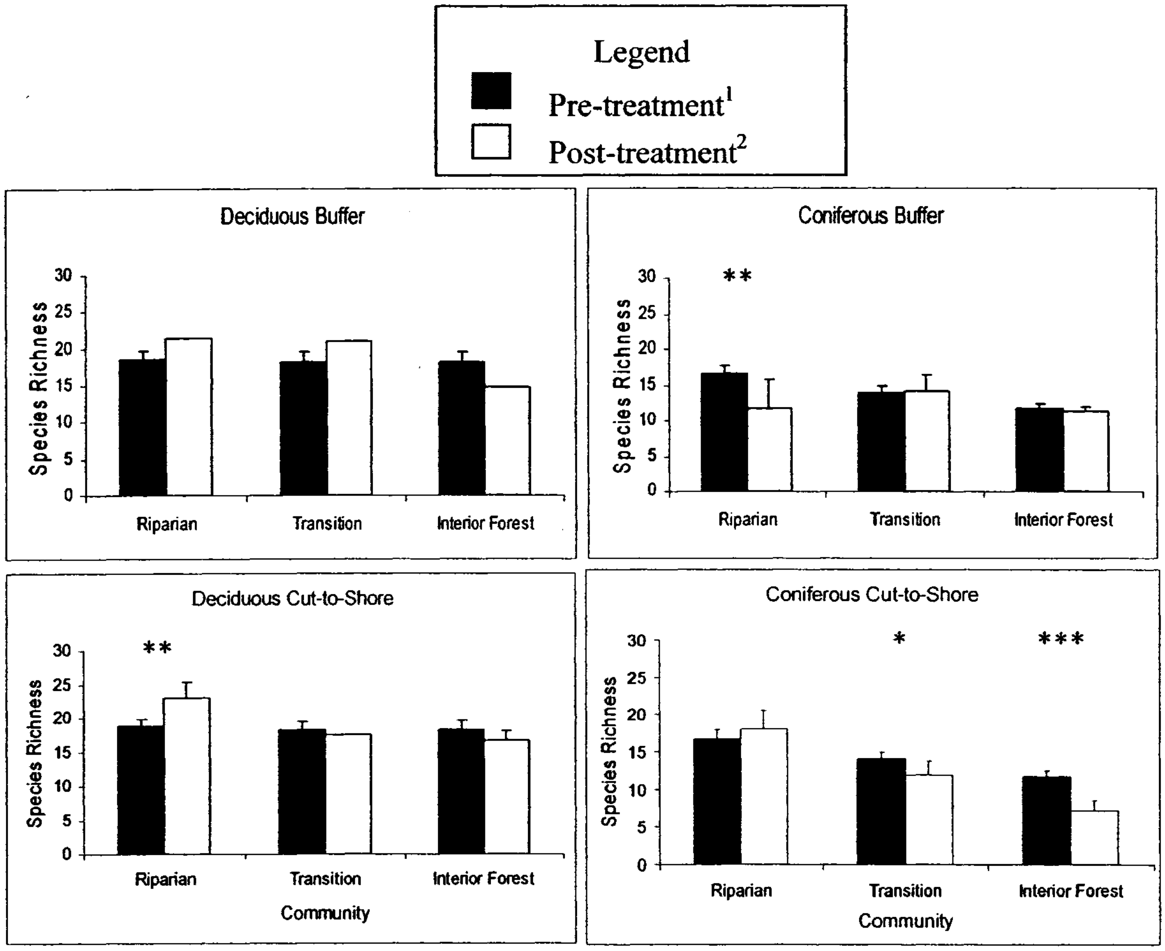

Figure 2.3. Mean ground vegetation species richness (with *SE*) pre- and post-treatment by community and stand class. [1]Means include all pre-harvest and 2003/2004 reference data, [2]one year post-harvest. Harvest treatments: buffer (30 m), and cut-to-shore. * $p < 0.05$, ** < 0.01, *** $p < 0.001$.

** See Appendices A and B for actual *t*-values and mean (*SE*) values, respectively.

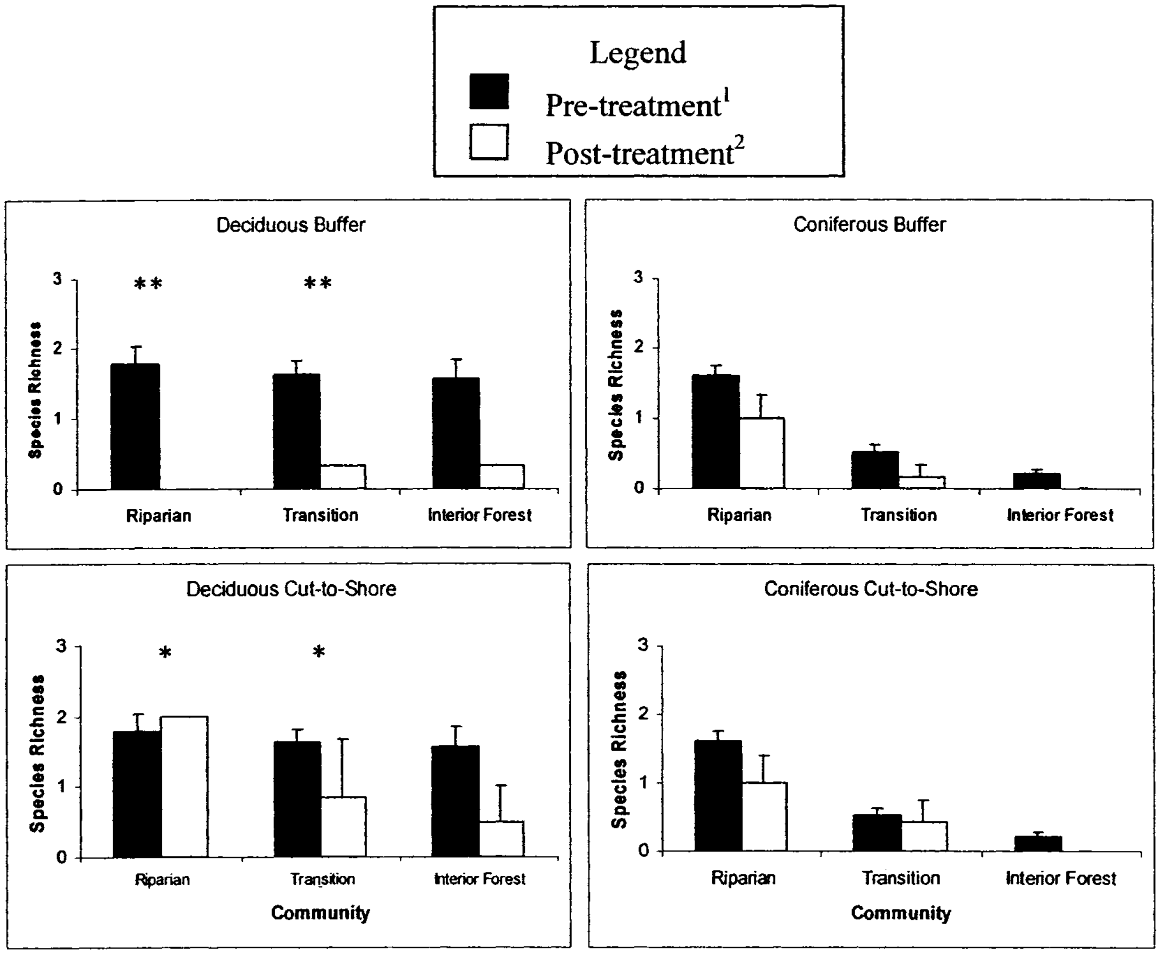

Figure 2.4. Mean low shrub species richness (with *SE*) pre- and post-treatment by community and stand class. [1]Means include all pre-harvest and 2003/2004 reference data, [2]one year post-harvest. Harvest treatments: buffer (30 m) and cut-to-shore. * $p < 0.05$, ** $p < 0.01$.

** See Appendices A and B for actual *t*-values and mean (*SE*) values, respectively.

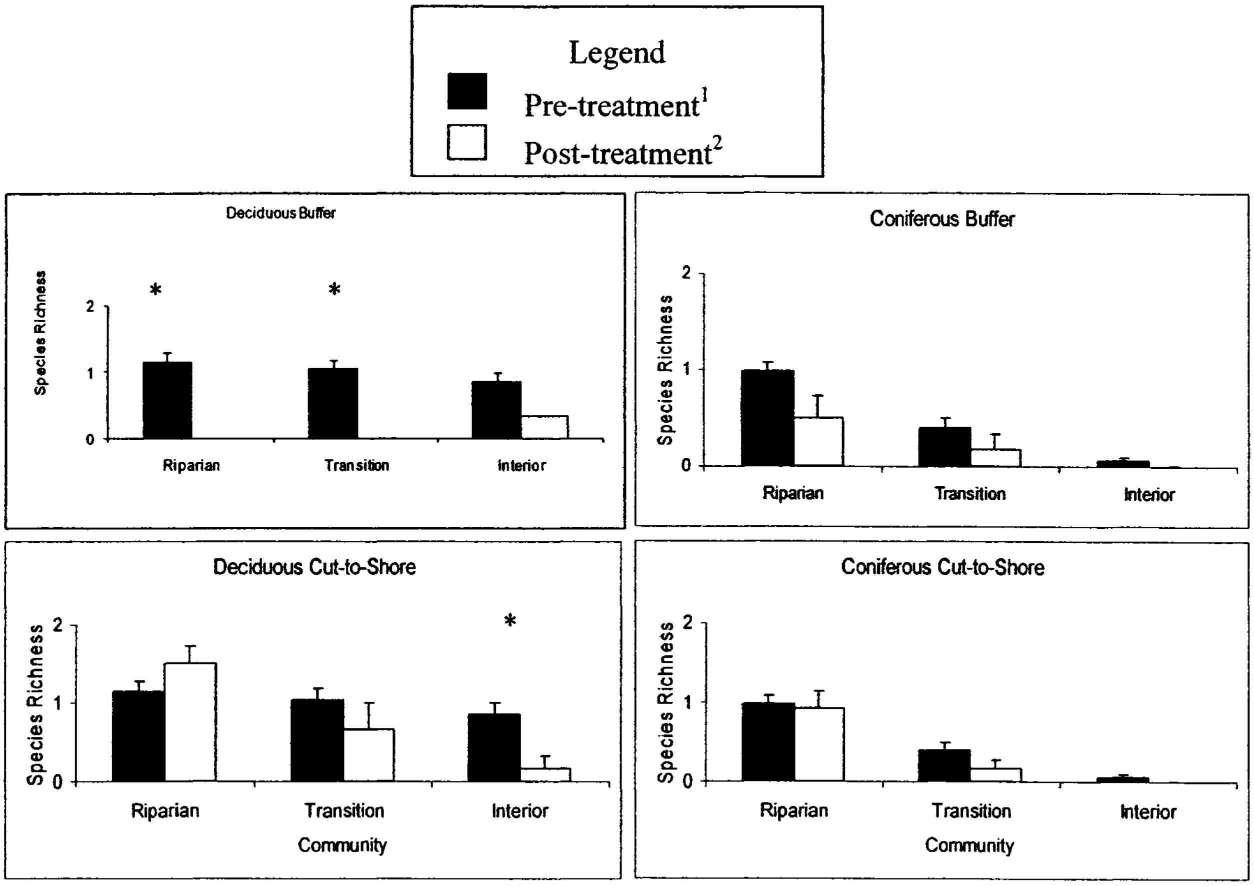

Figure 2.5. Mean tall shrub species richness (with *SE*) pre- and post-treatment by community and stand class. [1]Means include all pre-harvest and 2003/2004 reference data, [2]one year post-harvest. Harvest treatments: buffer (30 m) and cut-to-shore. * $p < 0.05$.

** See Appendices A and B for actual *t*-values and mean (*SE*) values, respectively.

2.3.5 Hypothesis 2a: For the tree layer in the absence of disturbance, there will be higher species richness in interior forest communities than in transition and riparian communities.

The nested ANOVA identified stand, but not community, as a source of variation. Mean species richness prior to harvest in the tree layer ranged from 1.8 to 3.3 (dark bars in Figure 2.6). Results of *t*-tests (Part A., Table 2.5) reveal that there were no community based differences in deciduous stands. In contrast, in coniferous stands, tree species richness in IF communities (3.3 ± 0.3) was higher than in T (2.7 ± 0.2; $p < 0.05$) and R communities (2.4 ± 0.3).

As with the LV and shrub layers, the hypothesis is supported in coniferous stands but not in deciduous stands. However, contrary to the patterns in GV, LS and TS, species richness in the tree layer increases with distance from the stream.

2.3.6 Hypothesis 2b: For the tree layer after harvest disturbance, there will be higher species richness in interior forest communities than in transition and riparian communities.

In the tree layer, only the deciduous, CTS treatment resulted in detectable differences. In this case, species richness declined from R to IF communities. The hypothesis is therefore not supported after disturbance.

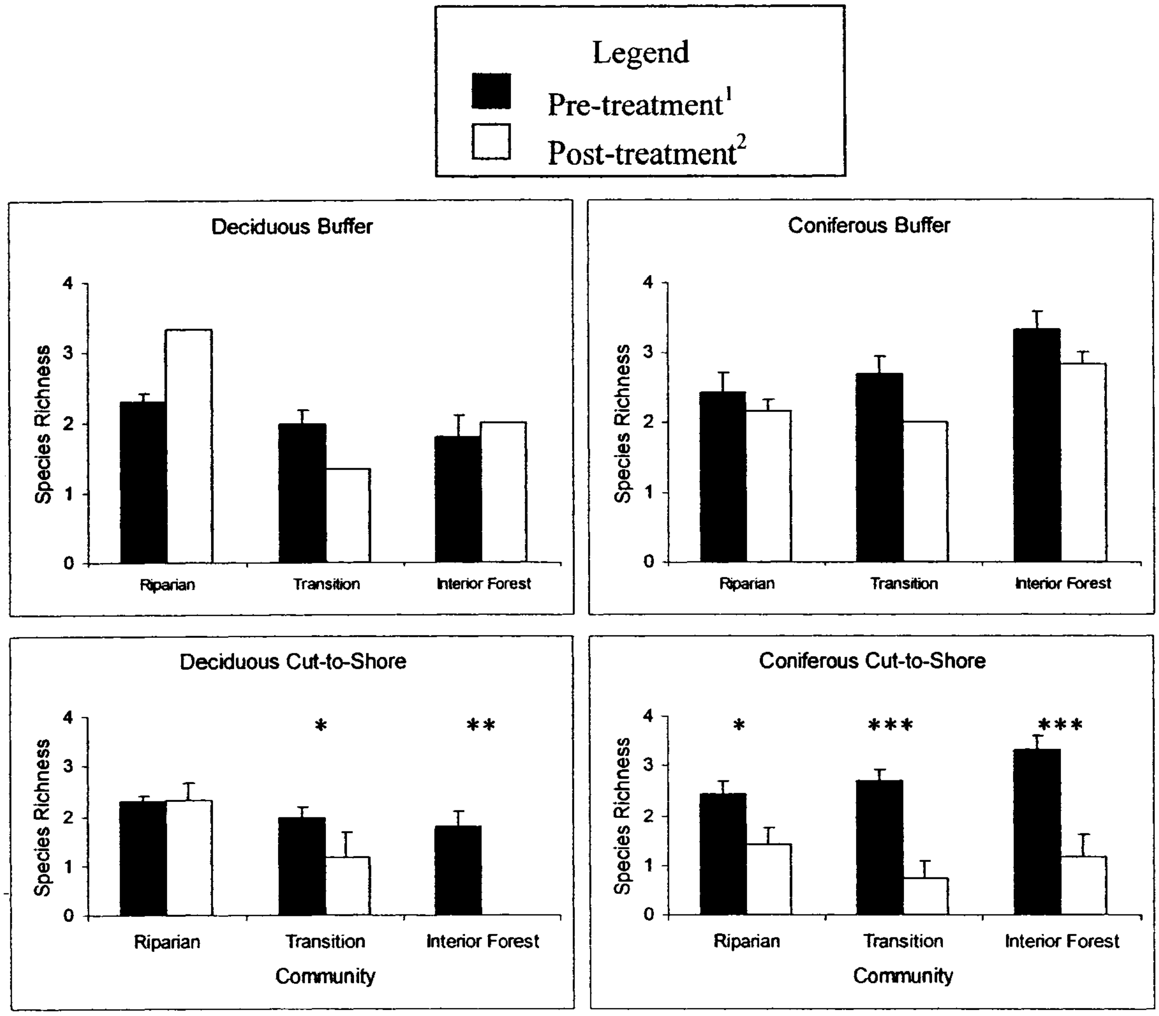

Figure 2.6. Mean tree layer species richness (with *SE*) pre- and post-treatment by community and stand class. [1] Means derived from all pre-treatment and 2003/2004 reference data, [2] one year post-harvest. Harvest treatments: buffer (30 m) and cut-to-shore: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

** See Appendices A and B for actual *t*-values and mean (*SE*) values, respectively.

2.3.7 Hypothesis 3: Harvesting reduces species richness in all communities and stand classes and cut-to-shore harvest more so than buffer harvest.

Results are divided into two parts: (1) comparison between reference and harvested communities and (2) comparison between the two harvesting methods.

2.3.7.1 Comparing reference to harvested stands

Ground vegetation layer

The number of species in the GV layer changed after harvest in four of the 12 communities studied (see Fig 2.3). In three coniferous communities (R, buffer; T and IF, CTS), the number of species declined however, in the R communities of the deciduous stands under CTS harvest, the number of species increased from 18.7 to 23.0 ($p < 0.01$). Non-significant increases were noted in the deciduous buffer, coniferous buffer and coniferous CTS. The hypothesis of reduced species richness following harvest is only supported in the coniferous stands.

Shrub layers

Following harvest, shrubs from both layers responded similarly within a stand class (Fig. 2.4 and 2.5). In coniferous stands, there were no detectable differences between pre- and post-harvest species richness values. The pattern of decreasing species richness from R to IF communities was maintained. In the case of deciduous stands, the type of harvesting affected the pattern of species richness. Under CTS harvest, species numbers increased slightly in the R communities and declined in the T (LS) and IF (LS and TS) communities. Under buffer harvest, species counts in all three communities dropped to zero or near-zero. As described in section 2.4, this decline is attributed to increased beaver activity following the removal of trees. As such, the hypothesis that there are more species pre-harvest is supported for deciduous stands only the R and T communities under buffer conditions and IF communities under CTS condition.

Tree layer

Figure 2.8 presents the results of *t*-tests between reference and harvested communities in each stand class. Somewhat surprisingly, even in the IF communities, there were no detectable patterns in species richness before and after buffer harvest. With the exception of the R communities of the deciduous stand class, specie richness under CTS harvest decreased in all communities. The hypothesis of fewer species following harvest is supported in the T and IF communities for both stands and in riparian communities of the coniferous stand class after CTS harvest, but not buffer harvest.

2.3.7.2 Comparing Cut to Shore and buffer harvesting

Ground vegetation layer

When effects of harvest on the GV layer were compared, there were three differences (Table 2.6). In coniferous stands, the number of species in R communities after CTS was higher than in buffer (21 ± 1.8 *vs* 12 ± 0.8, respectively ($p < 0.01$)). In coniferous IF communities and deciduous T communities, species richness under buffer conditions was higher than in CTS conditions (11 ± 0.6 *vs* 7 ± 1.1, respectively ($p < 0.01$) and 21 ± 1.8 *vs* 12 ± 0.8, respectively ($p < 0.01$)). The hypothesis of fewer species under CTS harvest is therefore supported in two instances out of six with respect to this layer.

Table 2.6. Results of the *t*-tests for differences between buffer (30 m) *vs* cut-to-shore harvest in the three communities in the four vegetation layers (*t*-values ranged from 0.00 to 5.29). All differences were significant at $p < 0.01$.

Vegetation Layer	Differences
Ground Vegetation	Coniferous Riparian Deciduous Transition Coniferous Interior Forest
Shrubs	Deciduous Riparian
Tree	Coniferous Transition Coniferous Interior forest Deciduous Interior forest

** See Appendix C for actual *t*-test values.

Shrub layer

Only two comparisons in the LS and TS layers are different. These are both found in the R communities of the deciduous stands and in both cases the species richness after CTS harvest is greater than that found after buffer harvest. The hypothesis of fewer species after CTS harvest is therefore not supported.

Tree layer

In the tree layer, differences between the two harvest methods were found in the IF communities of both stands as well as the T communities of the coniferous stand. In each case, species richness was less under CTS harvesting than under harvest with a buffer. The R communities, however, were not affected. The hypothesis of fewer species after CTS is supported in three of the six comparisons.

2.3.8 Hypothesis 4: Post-fire species richness i. follows the same patterns identified in hypotheses 1 and 2 and ii. will be higher in coniferous than deciduous affected by pre-disturbance stand class.

Six years after fire, two trends in community composition are evident from the information presented in Table 2.7 and Figure 2.7. First, gradients (richness declining with distance from stream) appear to have re-established in all layers of coniferous stands as well as in shrub layers of deciduous stands. Differences between communities were detectable for coniferous GV and LS as well as deciduous TS layers. Second, species richness in coniferous communities was less than that found in deciduous communities in ten of 11 possible comparisons (tree, TS, and GV predominantly). However, in the GV of the R communities, richness in the coniferous stands exceeded that of the deciduous stands.

In terms of the hypotheses posed with respect to recently burnt areas: 1) the patterns observed under CTS conditions related to: a) declining species richness with distance from the stream is supported for the GV and LS layers of coniferous stands and for the TS layers of deciduous stands and b) relatively similar species richness among the communities in the tree layers of coniferous stands is also supported. 2) species richness is affected by pre-disturbance stand class, but is not higher in coniferous stands than deciduous.

Table 2.7. Results for *t*-tests post-fire comparisons for coniferous and deciduous stands, all layers, and communities (riparian (R), transition (T), and interior forest (IF)).

Layer	Post-fire					
	Deciduous			Coniferous		
	R *vs* T	R *vs* F	T *vs* F	R *vs* T	R *vs* F	T *vs* F
Ground Vegetation	2.09	1.13	0.94	4.51***	5.68***	1.60
Shrub 1 to 3m	0.95	1.25	0.67	4.21***	3.34***	0.31
Shrub > 3m	0.50	4.00*	1.73	1.48	1.48	*na*
Tree	0.00	0.00	0.00	1.18	1.34	0.28

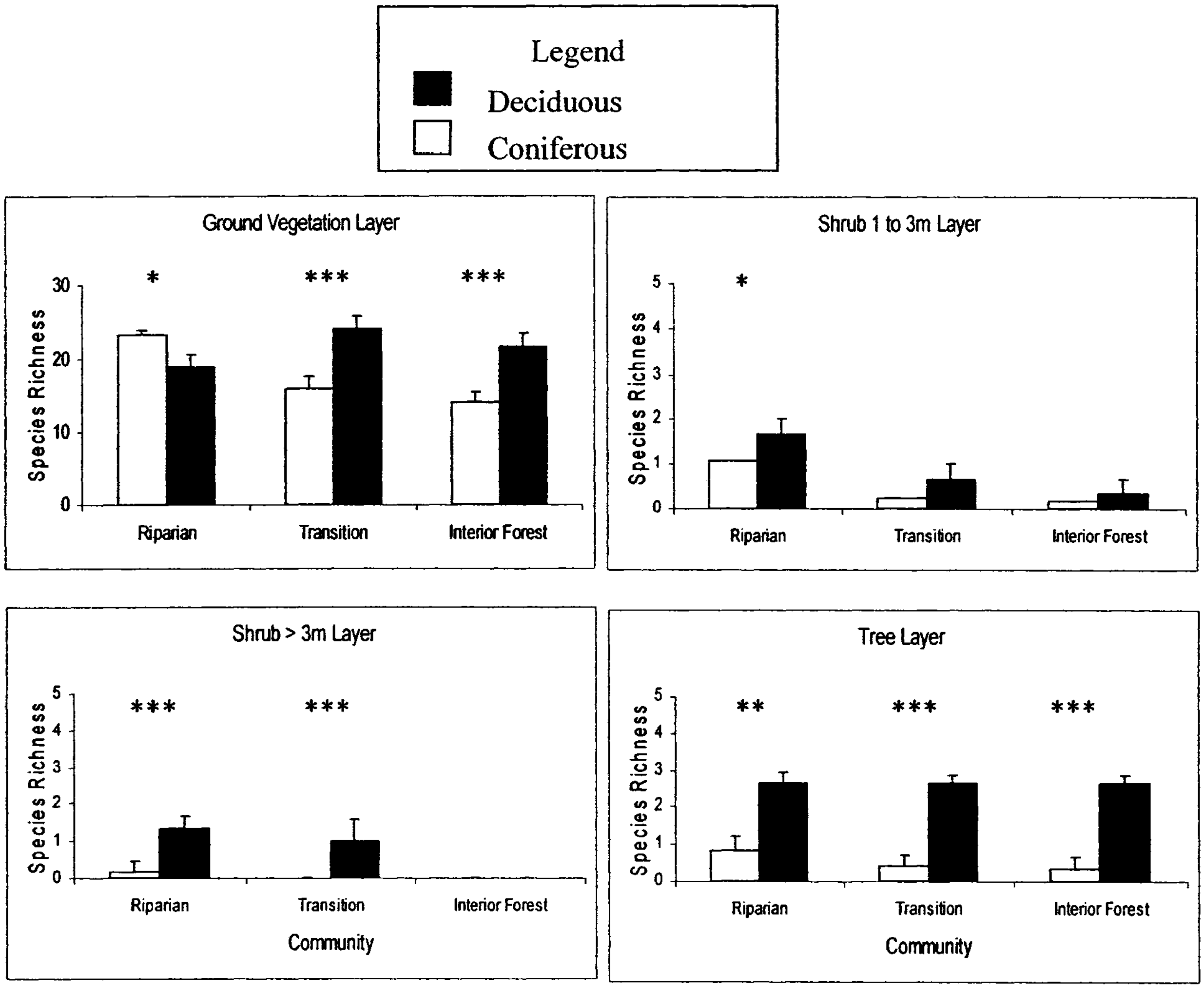

Figure 2.7. Mean species richness (with *SE*) of all layers for the fire treatment (6 years post-fire) by community and vegetation layer. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

** See Appendices D and E for actual *t*-values and mean (*SE*) values, respectively.

2.4 DISCUSSION

The vegetation communities of the Boreal Plain are increasingly exposed to anthropogenic disturbances (e.g., forestry, oil and gas). The hypotheses tested in the RVS were designed to capture pre-treatment conditions and describe baseline trends, as well as analyze how vegetation responded to forest harvesting (buffer and cut-to-shore) and fire disturbance. The RVS found distinct pre-treatment differences between coniferous and deciduous stands with regards to species richness patterns. deciduous stands remained relatively stable for all layers (GV, shrubs, tree) whereas, coniferous stands displayed a decreasing species richness gradient with distance from the stream channel for the shrub and GV layers. The difference in vegetation patterns observed between coniferous and deciduous stands affected how the different communities responded to the disturbances, especially the CTS treatment.

In the RVS, species richness in GV and shrub layers was higher in deciduous stands than coniferous stands. In addition, pre-treatment species richness in deciduous stands for all three communities was relatively constant, when compared to coniferous stands. A positive correlation between the presence of deciduous tree species and species diversity was observed by Berger and Puettmann (2000). However, Haeussler et al. (2004) suggested that microsite and site factors rather than overstory composition play important roles in determining species richness. Yet, with the exception of Mallik et al. (2001), boreal riparian vegetation species found within specific microhabitats are not well documented. Mallik et al. (2001) observed that many boreal species either increased or decreased strongly in abundance with distance from shore on relatively larger floodplains. Perennials (e.g., herbs and graminoids) displayed a stronger lateral gradient and increased in mean representation as the distance from the stream increased, when compared to annuals. Nonetheless, the RVS documented a consistent positive relationship between deciduous cover and species richness.

In the RVS pre-treatment, inter-community species richness patterns observed in coniferous stands were similar to those documented by Timoney et al. (1997). GV and shrubs generally decreased in species richness from R up through to IF communities. Further, in the RVS study all three communities were distinct. In contrast, shrub species richness, pre-treatment, in deciduous stands remained relatively constant from R to IF communities. The contrasting species richness patterns observed in the shrub layers of these stands were almost certainly related to light penetrating the tree canopy. Mature deciduous trees allow more light through their crowns when compared to coniferous trees. For example, in the same region of the RVS, Constabel (1995) documented that light transmission through coniferous trees was one-half to one-tenth to that of deciduous trees. Increased amount of light below deciduous canopies may have allowed for the shrub layers to persist in all three communities. On the other hand, in the coniferous stands shrub layers decreased in species richness as distance from the stream increased and the coniferous canopy became more dominant, limiting light penetration. The difference in the two shrub species patterns influenced the harvest effects observed in the stands. As noted, number of shrub species in deciduous stands was higher when compared to coniferous stands, in particular, in T and IF communities. As such, deciduous stands were more affected by forest harvest. In T and IF communities of coniferous stands, there were few if any shrubs and therefore there was little, if any, impact of harvest.

Identification of contrasting patterns of species richness within the shrub layers of both stands strengthens the need for site specific forest harvest and silvicultural guidelines. In the province of Ontario, for example, there are five different silvicultural guides for managing the variety of forest types (OMNR 2006), which allows for silvicultural flexibility. For instance, if shrub diversity in boreal forests is an important landscape component for a particular region then perhaps clearcutting may be acceptable for coniferous stands, but selective and/or shelterwood cutting might be more appropriate for deciduous stands to minimize the depletion of shrub species. In the province of Alberta, the Mixedwood Management Association is in the process of developing an ecologically based silviculture guide, the Alberta Boreal Mixedwood Silviculture Guide, that will be useful for all forested ecosystems within province boundaries. The guide will standardize data collection procedures, describe possible silvicultural treatments and treatment combinations, quantify the positive effects and mitigate the negative impact of those treatments (GDC 2003). Clearly, forest management in Canada is moving towards providing forest practitioners with references regarding silvicultural options for forest management and is linking these options to predicted outcomes.

Species richness in the deciduous tree layer pre-treatment remained relatively constant in all communities. In contrast, species richness in the coniferous tree layer of IF communities was higher than T and R communities. As expected, the tree layer for both stands was most affected post-treatment under CTS conditions compared to layers below. With the exception of the R communities in deciduous stands, CTS reduced tree species richness for both stands in all communities. Considering the nature of the harvest (clearcut) this was expected. In the absence of natural disturbances (e.g., fire, windthrow, and insect outbreak), silviculture treatments employed on harvested lands will determine forest trajectories for the next stand rotation.

In contrast to species richness patterns observed in the tree layer post-treatment under CTS conditions, GV was among the least affected in deciduous and coniferous stands. Reasons for this included: (1) The relatively high species richness measured in GV layers pre-treatment may have contributed to the lack of response observed, (2) harvest in the RVS occurred during winter and as such soil disturbance may have been limited when compared to areas harvested in summer, (3) in the CTS treatment, one year post-harvest is too early to detect changes in species richness. In northern Wisconsin in deciduous forests, uneven-aged and even-aged stands (10 and 40 years post-harvest, respectively) presented undetectable differences ($p < 0.05$) (Kern et al. 2006). However, due to the time-frame relating to the inventory, vegetation communities in that study may have already recovered. In contrast, in the RVS, the lack of response detected post-treatment under CTS conditions is most likely due to the post-treatment inventory being too early to capture treatment effects. During field inventory for the RVS, it was noted that individual specimens were struggling to survive. For example, in coniferous stands feather mosses were drying out because of the increased exposure to wind and solar radiation, however, they were still present one-year post-treatment under CTS conditions. A decrease in bryophyte species richness was expected following harvest (Hylander et al. 2002; Hylander 2005). In some coniferous sites inventoried in the RVS feather mosses made up the majority of the species present within plots, therefore, a shift in species composition following the first few years after the CTS treatment should be expected. Further, climatic variation will also influence species composition within these CTS stands post-treatment. For example, in deciduous stands species identified post-treatment that were not identified pre-treatment included: *Marchantia polymorpha, Brachythecium rivular,* and *Caltha palustris.* When weather data were compared between pre- and post-treatment years, there was more precipitation in the post-treatment year.

The ability of the buffer treatment to maintain species richness was accentuated in the tree layer, specifically in the T and IF communities and in the GV layer in IF communities. The tree layer was also the most affected post-treatment under CTS conditions, so these results were not surprising and are supported in the primary literature (Hylander et al. 2005). The ability of the buffer to maintain species richness in the shrub layers was not confirmed, largely due to local beaver influence. Beaver activity was greater in the buffer treatments than CTS treatments, especially after harvesting was implemented. Further, slope was greater in the CTS treatments, which hindered harvest operations up to the stream edge. In coniferous stands species richness post-treatment under both buffer and CTS conditions did not differ from pre-treatment conditions. Similarly, in a study in northern Sweden, no apparent edge effects were noted in the shrub layer of coniferous stands post-harvest (Hylander 2005). GV responses were limited in R and T communities compared to IF communities. IF communities of both stands, were mre species rich under buffer conditions when compared to CTS conditions suggesting the buffer treatment. In a study in northern Ontario on the Boreal Shield in boreal mixedwood stands no detectable changes in vascular plant species richness were documented (Lamb et al. 2003). In contrast, in northern Sweden, two to five years post-harvest, Hylander (2005) documented a decrease in bryophyte species richness, particularly along north facing conifer forest edges. With that being said, studies which document vegetation change over time post-treatment under buffer conditions are lacking, particularly during early successional stages and in deciduous stands. In the RVS site, as time passes and stands adapt to their new environment, it is expected that some new patterns will emerge, specifically in number of species in the GV layer.

Post-treatment, vegetation dynamics in fire treated stands had similarities when compared to what was observed and expected in the harvested stands. Species richness at the tree layer deciduous stands remained relatively constant among the three communities. In contrast, the coniferous stands were much slower to return six years post-fire. Fire intensity, which is influenced by relative humidity, may have been a contributing factor regarding the more species rich tree layer in the deciduous stands post-fire. With the exception of the bryophytes, the GV layer appeared to be more resilient to fire disturbance for both stands when compared to layers above. Excluding bryophytes, there is evidence that GV layers in coniferous stands are relatively well adapted to fire (Hamilton 2006). Further, in northern Ontario it has been documented that the number of vascular plant species present post-fire is generally highest within the first 10 years when compared to later successional stages (Shafi and Yarranton 1973). However, with regards to bryophytes, species richness increases as the stand ages. For example, in a study in northwestern Québec, *Hylocomium splendens* did not recolonize until 46 years post-fire and had the highest cover 167 years post-fire (DeGrandpré et al. 1993). In addition, in the RVS, the GV layer in deciduous stands appeared to be well established and had a greater number of species in T and IF communities than coniferous stands. This observation may also be a result of lower fire intensity within deciduous stands. The growth of deciduous shrub layers will most likely continue to limit light conditions on the ground, particularly in summer, the dominant growing season. As such, coniferous tree species that are more shade tolerant when compared to deciduous trees are probably more likely to become established under current conditions. The shift in species composition from a deciduous dominated tree layer to a coniferous dominated tree layer could change the trajectory of the stand when compared to pre-fire conditions.

2.5 CONCLUSIONS

The RVS found that deciduous and coniferous stands differ in species richness patterns, and that this difference effects how vegetation responds to disturbance. It also documents how biological influences (e.g., beaver) and local topography impact treatment effects. The deciduous stands had greater species richness and were more affected by the treatments and beavers than the coniferous stands. The coniferous stands had a natural gradient of decreasing species richness as the distance from the shoreline increased, making detecting harvesting treatments almost impossible. In contrast, the more species rich and relatively constant species richness gradient observed in deciduous stands provided a more sensitive environment than coniferous stands when detecting treatment effects. With respect to the fire disturbance, deciduous tree density was such that the shrub layer was suppressed while the GV returned to levels of species richness which were likely very similar to pre-treatment conditions. In contrast, coniferous tree and shrub layers were slower to return, however, the GV layer was uniformly well established six years post-fire.

It should be noted that there is scant literature documenting vegetation patterns of boreal headwater streams. Thus, river and lake publications have been utilized as necessary. Further, documentation of species richness patterns of boreal vegetation were more common in upland than riparian sites (e.g., Qian et al. 1998). Studies like this one contribute to the essential baseline inventory for boreal headwater systems.

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APPENDICES

APPENDIX A:

THE *t*-VALUES FOR HARVEST TREATMENT AND REFERENCE COMPARISONS

Table A.1. *t*-values for ground vegetation layer for all communities.

Stand	Treatment	Reference *vs* Treatment		
		Riparian	Transition	Interior Forest
Deciduous	Buffer	1.36	1.69	1.75
Deciduous	Cut-to-Shore	3.03**	0.01	1.21
Coniferous	Buffer	2.95**	0.22	0.54
Coniferous	Cut-to-Shore	0.98	2.13*	5.17***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table A.2. *t*-values for shrubs 1 to 3 m layer for all communities.

Stand	Treatment	Reference *vs* Treatment		
		Riparian	Transition	Interior Forest
Deciduous	Buffer	3.40**	3.06**	1.96
Deciduous	Cut-to-Shore	0.58	2.34*	2.30*
Coniferous	Buffer	1.43	1.18	1.01
Coniferous	Cut-to-Shore	1.84	0.44	1.42

* $p < 0.05$, ** $p < 0.01$

Table A.3. *t*-values for the shrub > 3 m layer for all communities.

Stand	Treatment	Reference *vs* Treatment		
		Riparian	Transition	Interior Forest
Deciduous	Buffer	2.73*	2.52*	1.12
Deciduous	Cut-to-Shore	1.12	1.14	2.10*
Coniferous	Buffer	1.61	0.77	0.62
Coniferous	Cut-to-Shore	0.27	1.07	0.88

* $p < 0.05$

Table A.4. *t*-values for the tree layer for all communities.

Stand	Treatment	Reference *vs* Treatment		
		Riparian	Transition	Interior Forest
Deciduous	Buffer	1.46	1.31	0.26
Deciduous	Cut-to-Shore	0.06	2.11*	2.97**
Coniferous	Buffer	0.40	1.33	0.92
Coniferous	Cut-to-Shore	2.14*	5.16***	5.44***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

APPENDIX B:

SPECIES RICHNESS MEANS AND *SE* VALUES FOR THE HARVEST TREATMENTS

Table B.1. Ground vegetation layer treatment means and *SE* for species richness in the riparian, transition and interior forest communities of the coniferous and deciduous stand.

Treatment	Community	Deciduous		Coniferous	
		Mean	*SE*	Mean	*SE*
Buffer	Riparian	21.3	0.0	11.8	4.0
	Transition	21.0	0.0	14.3	2.2
	Interior Forest	14.8	0.0	11.3	0.8
Cut to shore	Riparian	23.0	2.3	18.0	2.5
	Transition	17.5	0.0	11.9	1.9
	Interior Forest	16.7	1.3	7.2	1.3

Table B.2. Shrub 1 to 3 m layer treatment means and *SE* for species richness in the riparian, transition and interior forest communities of the coniferous and deciduous stand.

Treatment	Community	Deciduous		Coniferous	
		Mean	*SE*	Mean	*SE*
Buffer	Riparian	0.0	0.0	1.0	0.3
	Transition	0.3	0.0	0.2	0.2
	Interior Forest	0.3	0.0	0.0	0.0
Cut to shore	Riparian	2.0	0.0	1.0	0.4
	Transition	0.8	0.8	0.4	0.3
	Interior Forest	0.5	0.5	0.0	0.0

Table B.3. Shrub > 3 m layer treatment means and *SE* for species richness in the riparian, transition and interior forest communities of the coniferous and deciduous stands.

Treatment	Community	Deciduous		Coniferous	
		Mean	*SE*	Mean	*SE*
Buffer	Riparian	0.0	0.0	0.5	0.5
	Transition	0.0	0.0	0.2	0.2
	Interior Forest	0.3	0.0	0.0	0.0
Cut to shore	Riparian	1.5	0.2	0.9	0.3
	Transition	0.7	0.7	0.2	0.1
	Interior Forest	0.2	0.2	0.0	0.0

Table B.4. Tree layer treatment means and *SE* for species richness in the riparian, transition and interior forest communities of the coniferous and deciduous stands.

Treatment	Community	Deciduous		Coniferous	
		Mean	*SE*	Mean	*SE*
Buffer	Riparian	3.3	0.0	2.2	0.2
	Transition	1.3	0.0	2.0	0.0
	Interior Forest	2.0	0.0	2.8	0.2
Cut to shore	Riparian	2.3	0.3	1.4	0.3
	Transition	1.2	0.5	0.8	0.3
	Interior Forest	0.0	0.0	1.2	0.4

APPENDIX C:

THE *t*-VALUES FOR HARVEST TREATMENT COMPARISONS

Table C.1. Results for *t*-tests for buffer *vs* cut-to-shore treatments comparisons.

Stand	Vegetation Layer	Buffer *vs* Cut-to-Shore		
		Riparian	Transition	Interior Forest
Deciduous	Ground Vegetation	0.70	2.94**	0.83
Coniferous	Ground Vegetation	2.88**	1.95	3.00**
Deciduous	Shrub 1 to 3 m	5.29**	0.79	0.31
Coniferous	Shrub 1 to 3 m	0.00	0.62	*na*
Deciduous	Shrub > 3 m	4.58**	1.22	0.51
Coniferous	Shrub > 3 m	1.15	0.00	*na*
Deciduous	Tree	0.94	0.2	5.29**
Coniferous	Tree	1.03	2.90**	2.69**

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, *na* *t*-value could not be calculated.

APPENDIX D:

THE *t*-VALUES FOR INTER-COMMUNITY FIRE TREATMENT COMPARISONS

Table D.1. Results for *t*-tests for post-fire coniferous *vs* deciduous stand comparisons.

Layer	Post-fire Coniferous *vs* Deciduous Riparian	 Transition	 Interior Forest
Ground Vegetation	2.41*	6.68***	6.16***
Shrub 1 to 3 m	2.72*	2.15	0.53
Shrub > 3 m	6.75***	6.24***	*na*
Tree	4.01**	5.26***	7.22***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, *na* *t*-value can not be calculated.

APPENDIX E:

SPECIES RICHNESS MEANS AND *SE* VALUES FOR THE FIRE TREATMENT

Table E.1. Fire treatment means and *SE* for species richness for all layers in the riparian, transition and interior forest communities of the coniferous and deciduous stands.

Layer	Community	Deciduous		Coniferous	
		Mean	SE	Mean	SE
Ground Vegetation	Riparian	18.8	1.8	23.1	0.8
	Transition	24.0	1.4	16.0	1.6
	Interior Forest	21.7	1.8	14.1	1.5
Shrub 1 to 3 m	Riparian	1.7	0.3	1.1	0.1
	Transition	0.7	0.3	0.3	0.1
	Interior Forest	0.3	0.3	0.2	0.1
Shrub > 3 m	Riparian	1.3	0.3	0.2	0.3
	Transition	1.0	0.6	0.0	0.0
	Interior Forest	0.0	0.0	0.0	0.0
Tree	Riparian	2.7	0.3	0.8	0.4
	Transition	2.7	0.2	0.4	0.3
	Interior Forest	2.7	0.2	0.3	0.3