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O sweet spontaneous
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University of Alberta

Patterns of Riparian Disturbance in Alberta's Boreal Mixedwood Forest: Beavers, Roads, and Buffers

by

Kathryn Andrea Martell

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Conservation Biology

Department of Renewable Resources

Edmonton, Alberta

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University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Patterns of Riparian Disturbance in Alberta's Boreal Mixedwood Forests: Beavers, Roads, and Buffers submitted by Kathryn Andrea Martell in partial fulfillment of the requirements for the degree of Master of Science in Conservation Biology.

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Abstract

Road-crossings at streams in Alberta’s boreal mixedwood forest may act as human analogues of beaver dams by blocking flow, raising water tables upstream and lowering water tables downstream. I compared riparian vegetation on low-order streams with paired road crossings and beaver dams, to explore the idea that roads form a permanent, human-created beaver dam. My results indicate that water levels are raised upstream of road crossings but extensive interaction between road crossings and beavers confounded my analyses. Detailed field surveys of the beaver dams provided valuable data on beaver habitat use in boreal mixedwood forests. A 50-year chronosequence of air photos suggests that beavers may be the primary disturbance agent structuring riparian zones on low-order streams in the study area. Current forestry operating ground rules in Alberta require 30 – 60 m unharvested buffer strips on permanent streams but this study showed that beavers could be removing forest cover from entire buffer strips.

Acknowledgements

I am grateful to have had Lee and Steve as my supervisors, providing me with an appropriate mix of freedom to pursue the project as I saw it, a brainstorming platform and stats advice when needed, and homemade wine and music to keep me grounded.

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Chapter 1 Introduction and Methods

1 CONTEXT

In the past several decades, a regional-scale land-use change has taken place in northern Alberta. Rapidly expanding industrial activity – mainly forestry and petroleum product extraction – has brought extensive road networks, pipelines, well sites, seismic lines, and people to a region previously relatively undisturbed by human activity. This intensifying industrial activity is profoundly transforming a region that until recently was considered untouched wilderness (Schneider et al. 2003), where there have been few detailed studies of ecosystem processes, and even fewer addressing the impacts of anthropogenic use (Stelfox 1995).

Schneider et al. (2003) concluded that "the combined effects of the energy, forestry, and agriculture industries are threatening the integrity" of the western boreal forest. Based on conservative projections of current trends, they predicted that the cumulative industrial footprint in northern Alberta will quadruple over the next two or three decades. This industrial activity causes structural changes in the forest landscape – ranging from direct loss of forested land base, to changes in the species composition and age of remaining stands, to fragmentation effects from cutblocks and linear features – that can be expected to have significant, negative effects on wildlife and forest resources.

The Adaptive Management Experiment Team is an initiative advanced by the University of Alberta and Alberta-Pacific Forest Industries, Ltd. (AlPac) that addresses cumulative effects of human activities in the boreal forest. The AME group advocates a scientific framework of treating management strategies as experiments, evaluating ecological responses to management actions and then using this information to solve management issues: this approach is known as active adaptive management. The two key components of AME's work are developing models to predict effects of alternative management strategies, and conducting management experiments. Prior to initiating a large-scale experiment, the AME group is carrying out a set of linked *retrospective studies* to gain insights into key uncertainties regarding effects of current human disturbance.

This study of road-crossing impacts on streams and riparian areas in northeastern Alberta is a component of one of those retrospective studies.

2 STUDY RATIONALE

The western boreal forest region, as defined by Rowe (1972) in "Forest Regions of Canada", extends from southeastern Manitoba west through Alaska. Alberta's boreal ecoprovince comprises more than half of the land area of the province (Strong 1992). Regional vegetation is typically aspen-dominated, with mixedwood or coniferous stands at higher elevations or in wetlands (Rowe 1972, Strong 1992, AEP 1994a). Succession in upland forests is considered to lead from aspen (*Populus tremuloides*) and poplar (*Populus balsamifera*) stands, through mixedwood, to white spruce (*Picea glauca*) / fir (*Abies balsamea*) stands, however, as Rowe attests (1961), "the western boreal forest is a disturbance forest". White spruce and balsam fir are not well-represented in the mid-boreal mixedwood region due to frequent disturbances (Strong 1992). Stand-destroying disturbances such as fire, insect outbreak, windthrow, and flooding prevent continuous conifer-dominance and maintain a significant hardwood component in forest stands (Pojar 1996, Dix & Swan 1970).

Wetlands are prominent features of the boreal landscape (Strong 1992, AEP 1994a), comprising more than 50% of area in the boreal mixedwood regions of Alberta (Johnson et al. 1995). They provide critical habitat for migratory waterfowl and a large variety of other wetland-dependent wildlife such as moose (*Alces alces*), muskrat (*Ondatra zibethicus*), and passerine birds (Collins & Helm 1997, Mensing et al. 1998). Many of these wetlands are created and maintained by beavers (*Castor canadensis*), which consequently have been described as a keystone species in boreal forests of North America (e.g. Naiman et al. 1986, Pastor & Naiman 1992). Studies in other regions of North America have shown that dam-building and selective foraging can change hydrology, riparian community structure, and the availability of wetlands across the landscape; these effects can persist for decades or even centuries (Ruedemann & Schoonmaker 1938, Neff 1959, Hammerson 1994). Effects of beaver activity thus resonate throughout the landscape both spatially and temporally.

Across large tracts of Alberta's boreal mixedwood, the impacts of beavers are both striking and pronounced (Figure 1.1), although they have not been quantified nor studied in the primary literature. An extensive literature exists on a variety of aspects of beaver life history, impacts, habitat selection, and management, but most of these studies have been conducted in the northern US (Minnesota, Wisconsin, New York) and in northern Ontario and Québec. Alberta's boreal mixedwood ecoregions are quite different from these regions in forest species composition, climate, disturbance regime, and topography; therefore, there may be differences in beaver activity and effects. Beavers have been inadequately studied in northern Alberta despite their potential importance in structuring wetlands in the area.

Humans are another major modifying agent in boreal forests. Roads, forest harvesting areas, well sites, pipelines, and other infrastructures that accompany industrial resource extraction have become prominent features in northern Alberta. The impacts of roads in forest landscapes range from direct physical ones (such as geomorphic, geochemical and hydrologic changes), to indirect landscape level ones (aquatic habitat, terrestrial vertebrates, biodiversity), to socioeconomic effects (Gucinski et al. 2001). Road effects on geomorphic and hydrologic processes include chronic and long-term sediment inputs to streams, changes to channel morphology and flow regimes, and diversion of water from natural flowpaths (Gucinski et al. 2001). Despite over 50 years of research, industrial roads (i.e., roads whose primary use is by extractive resource industries such as logging, mining, and petroleum extraction) have been studied in very few places; almost all we know about forest roads in North America comes from studies in the Appalachians, Pacific Northwest, and Rocky Mountains. Worldwide, studies have been conducted almost exclusively in mountainous areas.

Few studies have examined road effects in areas dominated by snow precipitation, permafrost, and wetlands (Gucinski et al. 2001, Luce 2002). Little is known about how roads affect hydrology in areas of low topography such as northeastern Alberta. Air photo analyses of boreal Alberta seem to indicate that road-effect zones occur at stream crossings, with a "wet-up" effect upstream and a "dry-up" zone downstream. A few studies on this "road damming" effect where roads cross slowly-drained peatlands (Jeglum 1975, Stoeckeler 1965) documented changes to wetland type and vegetation composition up- and downslope of roads. Based on his research, Jeglum (1975) observed that “[t]he changes caused by the road damming are similar to those caused by beaver dams in that there are increased water tables behind the dam, and slightly drier conditions below it”. Unlike beaver dams, however, roads are essentially permanent features of the landscape; many of their ecological effects persist long after de-activation (Forman & Alexander 1998, Tague & Band 2001). The speculation that roads may function as a human analogue of beaver dams has never been investigated.

Figure 1.1 Effects of beaver dam-building and foraging across Alberta's northeastern boreal mixedwood forests, showing how foraging and chains of dams restructure riparian corridors

3 STUDY OBJECTIVES

The overall objective of this project was to compare the impacts of beaver dams and road crossings, in terms of wetland creation and effects on riparian areas, and to increase our understanding of beaver impacts in the boreal mixedwood forest.

Specifically, this project addressed the following questions:

1. Do road crossings alter riparian and aquatic habitats in ways similar to beaver dams?
2. How does beaver flooding and foraging alter the structure and composition of riparian areas in the boreal mixedwood of northern Alberta? and,
3. What are the implications of beaver activity for riparian buffer strips? Are policy modifications needed to address buffer strip management in response to beaver impacts?

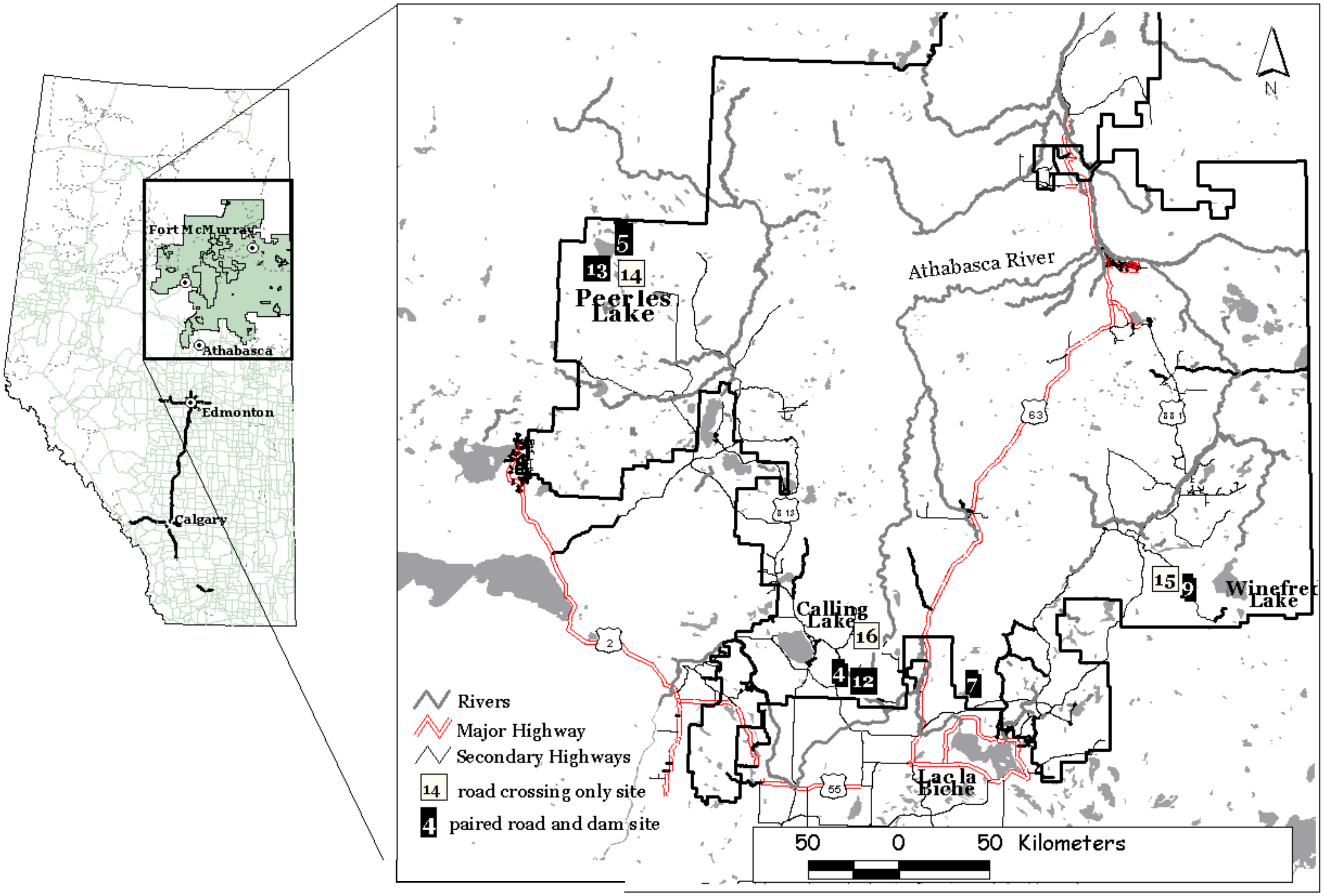
A better understanding of these two disturbance processes, beavers and roads, of the ways they may differ, and of the ways they potentially interact, will increase our ability to manage anthropogenic impacts in the boreal mixedwood.

4 STUDY AREA & METHODS

4.1 Study Area

My study area was the Forest Management Agreement (FMA) area of Alberta-Pacific Forest Industries Inc. (AlPac), a forestry operational area that covers 59, 054 km^2 in northeastern Alberta (Figure 1.2). Industrial activity in this region has expanded rapidly since construction of AlPac's mill in 1993. The FMA area is characterised by low topographic relief with extensive peatland complexes and by very long, cold winters, short, cool summers with long daylight periods, and relatively low annual precipitation that falls predominantly during the summer months. A number of classification schemes have been developed for Canada's boreal forests; I use Strong's (1992) classification of the ecoregions of Alberta. This study's sites mainly occurred in Strong's mid boreal mixedwood ecoregion. This ecoregion consists of broad lowland plains with discontinuous hill systems. Vegetation is typically aspen-dominated, with extensive mixedwood or coniferous stands (Rowe 1971, Strong 1992, AEP 1994a). Upland sites are dominated by pure and mixed stands of aspen and white spruce, with balsam poplar, black spruce (*Picea mariana*) and larch (*Larix laricina*) on lowland sites and pine (jack pine, *Pinus banksiana,* and lodgepole pine, *Pinus contorta*, and hybrids of the two) dominating drier sites (Strong 1992, AEP 1994a).

Figure 1.2 Alberta-Pacific Industries Forest Management Agreement Area in the context of Alberta, and approximate study site locations.



4.2 Study site selection

A site consisted of a paired road crossing and upstream active beaver dam. Site selection was based primarily upon road criteria. Crossings were sites where a one- or two-lane gravel road crossed a stream with a defined channel, with a culvert < 2.0 m diameter, and with flowing water at the time of sampling (Summer 2002). Selected sites had an active beaver dam 200 – 700 m creek distance upstream of the crossing. A dam was deemed 'active' if there were signs of dam repair or browsing from the year of field visit. I hypothesised that hydrological disturbance due to road crossings would be revealed through changes to riparian vegetation communities. Vegetation change would reflect long-term hydrologic alteration, and I therefore expected a time lag between road construction and community response. Such lags are known for vegetation communities responding to other types of disturbance (e.g. Milchunas & Lauenroth 1995) and to hydrological changes due to interruption of surface and groundwater flows by roads (Jeglum 1975). I initially intended to study only roads > 20 years old to overcome time lags in vegetation response; however, difficulties in finding enough appropriate sites forced me to use roads of a range of ages. There are few old roads in the study area and several of them have become major, paved highways. Drought conditions over the several years prior to field sampling, and large forest fires that season, further restricted the availability of sites by drying up or burning out entire creeks. In addition, the sheer volume of industrial activity on the landscape made it extremely difficult to locate stream crossings that did not have a harvested cutblock, pipeline, well site, or another road close to the stream. Many roads also had either a buried pipeline running alongside them, or such a wide roadbed or right-of-way that the crossing would not be easily comparable to a beaver dam. These difficulties finding enough appropriate sites resulted in a sample size of six paired sites, and an additional three road crossing-only sites (i.e., a road crossing with no associated upstream study dam). The study sites came from several areas of the FMA (Figure 1.2, Table 1.1).

Table 1.1 General, Legal, and GPS (NAD 1927) locations of study sites

Site	general location	legal location	GPS location road	GPS location dam ^
4	La Biche Wilderness	T70 R19 S14 w4	385904 6103481	386165 6103481
5	Peerless Lake	T89 R3 S31 w5	655858 6293323	656037 6293329
7	Heart Lake	T71 R13 S16 w4	440483 6111454	440408 6111559
9	Conklin	T76 R7 S22 w4	499627 6161550	499505 6161068
12	La Biche Wilderness	T70 R18 S24 w4	396621 6104822	396453 6105208
13	Peerless Lake	T87 R4 S9 w5	649662 6267769	649549 6267545
14*	Peerless Lake	T89 R4 S22 w5	650914 6289792	n/a
15*	Calling Lake	T71 R20 S12 w4	377024 6111460	n/a
16*	Conklin	T73 R20 S2 w4	375594 6129668	n/a

* site with road crossing only
^ measured from centre of dam

4.3 Field techniques

At each beaver dam or road crossing, 6 transects were laid out on one side of the creek, running perpendicular from water's edge into upland forest. At each dam or road crossing there were three upstream and three downstream transects, 3 m x 48 m, at 6, 21, and 36 m from the dam or road (at some sites the transect immediately up- or downstream (i.e. at 6 m) was placed 1 or 2 m further away to avoid wide rights of way). All transects began at water's edge. At some sites where the upstream pond was much wider than the downstream creek, downstream transects were offset by several metres from upstream ones.

All field data collection occurred June 9 to August 28, 2002.

The same side was sampled at both road and beaver sites along the same stream. Where possible, which side to sample was chosen randomly (by coin-toss), however in many cases one side of the creek was chosen to avoid other impacts such as cutlines, cutblocks, pipelines, well-sites, and other roads within 60 m of the stream. At several sites, either several plots or an entire transect could not be measured due to these other impacts.

Transects consisted of 16 consecutive 3 x 3 m plots. Within each plot I recorded species and diameter at breast height (dbh) for all trees and snags > 5 cm dbh; species and diameter at stump height (dsh, approx. 30 cm above ground) for all beaver stumps; and counted saplings (any stem < 5 cm dbh) for all tree species. Snags were recorded only to genus level. In many cases, a tree or stump could not be identified to species and was recorded only to genus. Beaver stumps were identified by height, and the characteristic toothmarks and conical shape of the cut. Only stumps > 1 cm diameter were measured. I also measured cover class for all tree, shrub, grass, and sedge species and for forbs, mosses, and lichens as groups. For each plot, I considered stem density and relative cover, and assigned the vegetation communities to meadow (grass & sedge), shrub, or forest categories.

At each road crossing, I measured culvert diameter, road width (width of gravel surface, not the entire roadbed), and stream depth and width at the upstream culvert opening. At beaver dams I measured the length of the dam and approximate pond size. Water depth at dams was taken by standing at the dam centre and measuring depth at approximately 1 m upstream from the dam. Depths were all conservative because the dam width was such that the bottom of the measuring stick was hitting the dam itself rather than pond bottom.

4.4 General site descriptions

Road width, stream characteristics, dam length, and pond size were variable among sites (Table 1.2, Table A1.1). Sites also differed in the relative dominance by deciduous or conifererous trees (Table A1.2) and understory composition (Table A1.3).

Table 1.2 Age and general descriptions of road crossings and beaver dams (see Appendix 1 for more details)

Site	road age (yr)~	road notes	dam distance from road (m)	dam age (yr)~	dam site notes
4	43	complex of old beaver meadows/breached dams upstream of road	300	35	dam is a recently rebuilt breach in an old overgrown dam
5	15	evidence of old impoundment at road, currently small pond ~ 4m x 6m	200	14	dam is recently rebuilt breach in old overgrown dam, lodge in pond
7	9	evidence of old impoundment at road, also beaver exclusion device; evidence of old beaver activity downstream of road	240	12	another dam about 60 m upstream of dam site
9	22	several old breached and a couple of newly-built dams between road and dam site	620	<1	dam freshly built, area newly flooded, flooded aspen still have green leaves
12	34	several old breached and a few newly-built dams between road and dam site; road has 2 culverts, one above the other	640	5	dam freshly built
13	30	wide right of way upstream of road crossing; big plunge pool and sloughing banks on downstream side of road crossing	220	1	dam freshly built, area newly flooded; older, active dams upstream of dam site, first one about 40 m upstream
14*	15		n/a	n/a	road only -- lots of breached dams upstream but no fresh activity
15*	25	several old dams within 40 m of road crossing	n/a	n/a	road only -- no fresh activity, big willow flats ~150 m upstream
16*	10	old breached dam several hundred m upstream, no fresh activity	n/a	n/a	road only -- dam with old lodge and huge wetland about 1 km upstream but no fresh activity

~ approximate age, see Chapter 3 for methods of determining age

* site with road crossing only

5 THESIS OUTLINE

This chapter has presented an overall introduction to the rationale and objectives of this study, as well as describing field methods. Chapter 2 contains a more extensive literature review of relevant topics including vegetation succession theory, riparian ecology, and keystone species concepts. The subsequent chapters have more detailed reviews of topics relevant to their specific foci. Chapter 3 is an analysis of temporal change at my study sites, using a chronosequence of air photos. In this chapter I also link this time series analysis to foraging data from the field survey, to address the issue of beaver impacts on riparian buffer strips and implications for forest management objectives in Alberta. In Chapter 4, I analyse possible hydrologic interruptions at road crossings and compare these effects to those of beaver dams, and examine some questions about beaver ecology in relation to road-crossing structures. Chapter 5 is an analysis of beaver-caused changes to riparian areas surrounding their dams, including natural history data of beaver habitat use and ecology in boreal mixedwood forests, an area where they have not yet been studied. Finally, Chapter 6 is a synthesis of results, with overall discussion and conclusions, management recommendations in relation to current forest policy, and suggestions for future research. A full reference list is provided in Chapter 7.

Chapter 2 Literature Review

1 SUCCESSION, DISTURBANCE, AND BOREAL FORESTS

1.1 Boreal Mixedwood Forests

Boreal forests are the most extensive ecoregion of North America, covering nearly half of the continent north of Mexico (Pojar 1996). The western boreal forest extends from southeastern Manitoba west through Alaska, and is physiographically and geologically very different from boreal regions of eastern North America (Pojar 1996). Alberta's mid boreal mixedwood ecoregion is typically aspen-dominated, with mixedwood or coniferous stands at higher elevations or in wetlands (Rowe 1971, AEP 1994a). Generally, succession in these boreal forests is said to lead to white spruce / balsam fir (*Abies balsamea*) stands. Many researchers question the applicability of succession theory to boreal forests, however, because stand-destroying disturbances such as fire, insect outbreak, windthrow, and flooding prevent conifer-dominance and maintain a prominent hardwood component (Dix & Swan 1970, Pojar 1996).

1.2 Succession & Disturbance theory

The concepts of disturbance and succession are intricately linked. Succession has been defined as "the changes observed in an ecological community following a perturbation that opens up a relatively large space" (Connell & Slayter 1977). Early studies described the sequence of species that successively invade a site and Clements (1916) proposed a theory that the earliest species modify the environment so that it is more suitable for species later in the succession trajectory. Despite doubters, dissenters, and disputes, both at the time (e.g. Gleason 1917) and since (e.g. Whittaker 1953, Connell & Slayter 1977), this theory of the causes and culmination of succession took a firm hold in North American ecology. The counter-view put forward by Gleason (1917) is that a community is simply composed of whichever species arrive at the site first, and the sequence of species is determined solely by their life-history characteristics (there is no 'facilitation' mechanism by previous species). A third model, and the one for which there is the most empirical support and acceptance in the scientific community, holds that all species exclude or inhibit later colonists until they die, thus freeing resources, and only then can later colonists reach maturity (Connell & Slayter 1977).

Although Clements' 'facilitation' model has largely been discredited (Whittaker 1953, Connell & Slayter 1977), his legacy is an enduring and ingrained perception of succession as an orderly, deterministic sequence of communities leading towards a self-perpetuating 'climax' stand where further change occurs only on a small scale as individuals die and are replaced. This directional view of succession sees disturbance as a process that "resets" the sequence, returning the community to an earlier stage (Levin & Paine 1974, Connell & Slayter 1977), "a mechanism resetting the inexorable march toward equilibrium" (Pickett & White 1985b). From this view we have a distinction between "primary" succession – beginning from bare, mineral soil – and "secondary" succession, which proceeds from a point intermediate along the successional pathway.

Calling himself a "botanical atheist", Egler (1947) expressed the frustration of many ecologists when he wrote,

> "The term Succession, in the minds of some, appears to denote a succession of step-like metamorphoses from one association to another. Furthermore, the retrogressive-progressive argument makes it necessary for one to know whether he is "coming" or "going", a stand which the writer cannot always take… , and which others usually settle more by faith than by empirical knowledge."

At the same time, Watt (1947) proposed "cyclic succession" of phases of plant communities, and the concept of succession has largely evolved to "be thought to occur, not as series of distinct steps, but as a highly variable and irregular change of populations through time, lacking orderliness or uniformity in detail, though marked by certain fairly uniform over-all tendencies" (Whittaker 1953). In this context, disturbance is seen not as a simple mechanism resetting patch age but rather, as a process with a major rôle in shaping ecosystem structure and composition (Connell 1978, Sousa 1984, Petraitis et al. 1989, White & Jentsch 2001).

1.3 Disturbance in boreal ecosystems

Traditionally, disturbances were viewed as uncommon, irregular events that cause abrupt structural changes in communities, moving them away from near equilibrium conditions (Sousa 1984). This view is predicated on the theory of a self-perpetuating, pre-determined climax state as the inevitable result of succession. The climax is perhaps one of the most disputed concepts in ecology and has progressed from Clements' monoclimax through Tansley's polyclimax (Tansley 1935), with every conceivable variation (and some perhaps quite inconceivable ones; see Whittaker 1953 for an interesting review). More recent theories appreciate that disturbances are ubiquitous and inherent features of natural communities, and define them as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White & Pickett 1985). This view asserts that climax communities may not exist, and that disturbance is often patchy, distributed in time and space, variable in impact and magnitude, and is entirely dependent upon the scale of study (Pickett et al. 1989) and the state of the community prior to disturbance (White & Pickett 1985). Two or more disturbance agents may interact, often in unexpected ways (Paine et al. 1998), and this interaction may be more important in shaping communities than any single disturbance (Runkle 1985).

Ecologists have classically only considered large-scale disturbances; in North American boreal forests, this has meant a near-myopic focus on the effects of fire. Recently, there has been a growing recognition of the importance of small-scale, within community disturbances ("gap dynamics") both in general (Runkle 1985, Schaminée et al. 2002) and in the boreal forest, where researchers have demonstrated the importance of gaps due to flooding and ice scour (Helm & Collins 1997), small fires (Kuuluvainen 1994), insects outbreaks (Kneeshaw & Bergeron 1996), storm-caused tree mortality (Hytteborn et al. 1987), and herbivory (Pastor et al. 1988, Riggs et al. 2000).

In boreal forests, gap dynamics may have important consequences for within-stand succession. Gaps are critical for conifer invasion in young aspen-dominated stands (Kneeshaw & Bergeron 1998) and for maintaining a deciduous component in older, coniferous stands (Hytteborn et al. 1987, Kneeshaw & Bergeron 1998). The outcome of small-scale gap succession is largely unpredictable, however, since seedling abundance is linked to abundance of parent trees, stand type, abiotic characteristics, and gap-size (Kneeshaw & Bergeron 1996, Greene 1999). Thus, these secondary disturbances may modify or even control stand dynamics between fire events.

In light of the over-arching impact of fires and the importance of stand type and chance in determining stand composition, the western boreal forest has been described as a "disturbance forest" (Rowe 1961), where succession is relatively unimportant and "any attempt to fit the vegetation into the mold of a climax concept would be unreal and … unjustified" (Dix & Swan 1970). Boreal forest landscapes are a mosaic of forest types, that can be either transitional or relatively permanent (Rowe 1961, Johnson et al. 1995), due to either recurring disturbance (Dix & Swan 1970, Elliott-Fisk 2000) or self-perpetuation through vegetative sprouting (Elliott-Fisk 2000). For these reasons, researchers question the traditional viewpoint of closed spruce or fir forest as the climax stage of boreal succession and advocate a dynamic, multi-path succession model as more realistic than orderly successional dogma.

At its heart, the theory of succession seeks to explain community change over time and space and observed dominant regional vegetation. Succession can be seen as change in plant communities over time according to changing abiotic factors and the species' life histories. Whether or not the process always goes through the same stages, whether or not disturbances 'interrupt' the process, over time the effects of climate, geology, and tree longevity in the boreal forest lead to a shift from aspen-dominated stands to coniferous stands. Aspen, poplar, and other pioneer deciduous species colonise large open areas; shade-tolerant conifer understories develop under mature deciduous canopies; and over time, as the short-lived aspen and poplar die, these conifers grow to maturity to create a conifer-dominated stand (Nanson & Beach 1977, Strong 1992, AEP 1994a). While this conifer forest may not be a "stable" or self-perpetuating climax à la traditional succession theory, it concludes the overall sequence of community change in western boreal forests, in the absence of disturbance. Some would argue that for boreal mixedwoods, you cannot put in the caveat "in the absence of disturbance" because it is such critical and pervasive process; I agree with Whittaker that plant community succession is a route of irregular community change through time that is marked by overall tendencies and patterns (perhaps it flows as a braided stream, with oxbows and back channels, and not as a straight river, but its overall direction of movement is still from headwaters to the sea).

2 STREAM ECOSYSTEM THEORY

2.1 To continuum or not to continuum?

In the past several decades, there have been numerous attempts to develop generalised theories of structure and function in aquatic systems. The most prevalent of these was the river continuum concept (RCC) developed by Vannote et al. (1980), which treated streams as longitudinally linked systems where ecosystem processes are defined by the unidirectional flow of water and materials. The RCC was later adapted to consider discontinuities due to regulation (Ward & Standford 1983a, Stanford et al. 1988) and changes in landforms and hydraulics (Sedell et al. 1989), to encompass broader spatial scales (Minshall et al. 1985), to address lateral linkages between the channel and riparian systems (Naiman et al. 1988a), vertical and temporal dimensions (Ward 1989), and to examine the effects of anthropogenic activities (Stanford et al. 1988, Cummins et al. 1984).

The RCC has thus flowed through the “serial discontinuity” (Ward & Stanford 1983a) and “flood pulse” (Junk et al. 1989) concepts, to embrace the watershed approach (Minshall 1988, Tockner et al. 2000) and arrive at the current vogue model of “hierarchical patch dynamics” that describes each stream network as a patchy discontinuum from headwaters to mouth, driven by hierarchically nested and interacting elements and processes (Naiman et al. 2000a, Poole 2002). This most recent incarnation arises from application of landscape ecology ideas to lentic and lotic ecology theory, and is perhaps an excellent example of the “intellectual baggage” Minshall (1988) denounces in stream ecosystem theory – the legacy from having basic tenets of modern stream ecology proposed and promoted by geomorphologists and terrestrial ecologists, rather than by aquatic ecologists.

2.2 Serial discontinuity in context

Theories of stream ecosystem function largely grew out of studies on, and speculation about, small headwater streams in North America. Later attempts to include large-river dynamics led researchers in other areas to point out that large, unaltered river systems are a rarity in the developed world – rivers simply do not flow as uninterrupted continua. The "serial discontinuity concept" thus proposed that regulation by dams and weirs creates a series of alternating lentic and lotic reaches (Ward & Stanford 1983a).

This theoretical perspective of anthropogenically-regulated rivers grew from an understanding that disturbances disrupt major interactive pathways in stream ecosystems just as they do in terrestrial ones (Ward & Stanford 1983b, Ward 1989). Furthermore, ecologists recognised the importance of natural abiotic and biotic discontinuities – changes to channel morphology, landforms, and hydrology (Stanford et al. 1988, Sedell et al. 1989), that make a river system a sequence of patches of varying lengths and widths. Even unaltered streams, therefore, are "serially discontinuous", and lotic systems can be seen as a collection of "resource patches" separated by boundaries (Naiman et al. 1988a). These influential patches extend to the connections between each stream and its surrounding riparian system, not only through the influence riparian vegetation can have on hydrology and channel morphology (Naiman et al. 1988a, Naiman & Décamps 1997) but also because of the importance of riparian vegetation to lotic nutrient cycling (Cummins 1974). Riparian patch dynamics will thus affect lotic food webs in terms of quantity and quality of leaf litter (Cummins et al. 1984, Pringle et al. 1988).

Despite this consideration of natural discontinuities along stream corridors, few ecologists have included an explicit consideration of beaver effects as patch occurrences in the context of stream ecosystem theory (Smith et al. 1991, Pringle et al. 1988). Beavers create discontinua both by building dams and creating ponds, and by foraging in the riparian areas surrounding them, producing "a startling array" (Pringle et al. 1988) of different patches within a drainage network.

Roads, too, can serve to disconnect, not only isolating streams from their flood plains but also blocking movements of animals and plants (Pringle 1997, Gucinski et al.

2001). Road crossings at streams can affect fish migration, invasion by exotic species (Gucinski et al. 2001), alter channel morphology (Lyons & Beschta 1983, Wemple et al. 2001) and hydrology (Tague & Band 2001, Gucinski et al. 2001), and convert subsurface to surface flow (Stoeckeler 1965, Megahan 1972). In addition, roads may alter other processes of patch formation in stream networks: at a landscape scale, roads can change the timing, frequency, and magnitude of floods and debris flows (Jones et al. 2000, Nakamura et al. 2000, Wemple et al. 2001) suggesting that roads influence disturbance regimes of aquatic habitats (Gucinski et al. 2001). These observations led Trombulak & Frissell (2000) to speculate that roads cause "aquatic fragmentation" – a concept analogous to discontinuity theories of stream ecosystem function.

3 RIPARIAN ZONES

The riparian zone is defined as "the stream channel between the low and high water marks and that portion of the terrestrial landscape from the high water mark towards the uplands where vegetation may be influenced by elevated water tables or flooding and by the ability of the soils to hold water" (Naiman & Décamps 1997). Essentially, it is the vegetation zone surrounding streams and lakes and that is influenced by them to create a different plant community than surrounding upland areas.

Riparian plant communities are 3-dimensional zones of interaction between terrestrial and aquatic systems (Gregory et al. 1991, Naiman & Décamps 1997)(four dimensional if we consider temporal factors as well, Ward 1989), generally composed of an unusually diverse array of species and processes compared to uplands (Naiman et al. 1993). Due to their structural and compositional diversity (Naiman & Décamps 1997, Harper & MacDonald 2001), their rôle as movement corridors for plants and animals (Gregory et al. 1991, Naiman & Décamps 1997), and their importance in maintaining different populations of plants (Suzuki et al. 2002) and animals (Whitaker & Montevecchi 1997, Darveau et al. 2001) than upland areas, riparian zones are a critical component maintaining regional biodiversity (Naiman et al. 1993). Riparian zones thus contribute substantially to alpha, beta and gamma diversity and their regional importance far exceeds their relative proportion of the landbase (Gregory et al. 1991).

In general, riparian zone width along streams is related to stream size, position in drainage network, hydrologic regime, and local geomorphology (e.g. Naiman & Décamps 1997). Frequent disturbances (floods, ice scour, debris jams), in conjunction with environmental gradients (moisture, light levels) create small and discontinuous patches that lead to diverse plant communities in different successional stages. Riparian vegetation is thus influenced by both local- and landscape-level factors.

3.1 Succession in riparian zones

Riparian areas, in general, experience frequent disturbances of varying intensity and duration, leading to patches of vegetation of differing age, species composition, and structure (Naiman & Décamps 1997, Bendix 1997). While this diversity is responsible for the regional importance of riparian zones in maintaining biodiversity, it also makes it difficult to make definitive statements about succession in riparian communities. Generally, disturbances such as flooding expose bare mineral soil that is rapidly colonised by sedges and grasses; over time, this meadow stage is replaced by a shrub stage (typically genera such as willows (*Salix*) and alder (*Alnus*) which are tolerant of high water table and exposure); and, ultimately, trees. Riparian community succession thus proceeds from meadow, through shrub, to forest. Frequent disturbances often “interrupt” this process and maintain meadow and shrub zones along riparian corridors (Walker et al. 1986, Naiman & Décamps 1997).

3.2 Landscape-scale factors influencing riparian vegetation

At a broad-scale, riparian vegetation patterns are determined by sedimentary landform types, elevation, and soil characteristics (Hughes 1997, Naiman & Décamps 1997). Most studies of riparian systems highlight the importance of disturbance in structuring vegetation. Disturbances such as flooding (e.g. Hughes 1997, Bendix & Hupp 2000) and ice scour (Helm & Collins 1997) interact with underlying geomorphological characteristics (Robertson & Augsperger 1999, Fischer et al. 2000) to create plant communities in a mosaic of different successional stages along rivers and streams (Jansson et al. 2000, Suzuki et al. 2002).

Although riparian diversity may ultimately depend on disturbance regime, the relationships are unpredictable and details of individual stream networks are key (Bendix 1997), especially where susceptibility to disturbance is unevenly distributed across the landscape due to changes in abiotic factors (Fischer et al. 2000). Recent landscape-level research shows that, at a regional scale, diversity may be strongly controlled by anthropogenic activities (forest and river management) (e.g. Bendix 1994, Decocq 2002). Anthropogenic disturbances on surrounding watersheds may have a greater potential for inducing enduring changes to the structure and function of riparian-stream systems than disturbances within the riparian systems themselves, for example through changing regional flood regimes (Rood & Heinze-Milne 1988, Rood & Mahoney 1990, Clary et al. 2000).

3.3 Local-scale factors influencing riparian vegetation

At the patch level, most researchers conclude that riparian vegetation communities are largely determined by abiotic factors, mainly soil moisture, light, and flooding (Decocq 2002, Harper & MacDonald 2001). Disturbance frequency and moisture gradients play key rôles in determining vegetation composition (Naiman et al. 2000a) but vegetation patterns reflect a subtle combination of overlapping gradients (Bendix 1994, Hughes 1997, Shafroth et al. 2002). While disturbance regime determines the age of vegetation patches, individual species life history characteristics shape patterns of species arrival and change (Nanson & Beach 1977, Walker et al. 1986, Jansson et al. 2000) and both local and landscape variables are important to explain local seedling occurrence (Walker et al. 1986, Dixon et al. 2002). Seed and seedling abundance are linked to forest composition (Walker et al. 1986) but stochastic and edaphic factors exert a strong influence on community structure over time (Bendix 1994, Tabacchi et al. 1996, Helm & Collins 1997, Harper & MacDonald 2001).

Although the effects of herbivores on plant communities have been extensively studied in other systems, they have rarely been examined specifically in riparian ones (except for beavers). Grazing can alter spatial heterogeneity of vegetation, influencing ecosystem processes and diversity (Helm & Collins 1997, Adler et al. 2001). Through selective browsing, moose change plant communities and ecosystem properties in boreal forests (Pastor et al. 1988) and ungulates in general are viewed as agents of chronic disturbance influencing succession, nutrient cycles, and soil properties (Huntly 1991, Riggs et al. 2000). In one study examining interacting influences on riparian vegetation, herbivory by moose was a major factor regulating successional pathways (Helm & Collins 1997). The influence of beavers on riparian communities and succession dynamics is well-studied. Tree-felling and pond-building create and structure meadow and shrub communities in riparian corridors (e.g. Pastor & Naiman 1992, Johnston et al. 1993), alter riparian forest composition (e.g. Donkor & Fryxell 1999, Barnes & Mallik 2001), and beaver herbivory can change macrophyte composition in ponds (Ray et al. 2001). These effects are strongly site-dependent (e.g. Jenkins 1975, 1980) and may also depend on underlying edaphic patterns (Donkor & Fryxell 2000).

3.4 Intersecting influences & scales

Essentially, riparian community composition at any particular point represents a unique intersection of influences operating at different scales (Bendix 1994). Many environmental gradients influence riparian vegetation at both micro- and macroscales (Jansson et al. 2000, Decocq 2002) and different vegetation layers respond differently to environmental factors (Decocq 2002). These factors show significant landscape x local interactions, indicating that the influence of some local factors may depend on landscape context (Tabacchi et al. 1996, Dixon et al. 2002). Species diversity and overall community composition therefore depend on simultaneous effects of regional (river-independent) and local, river-dependent factors.

There appears to be a chasm between the findings of riparian researchers and those of beaver researchers. While studies of beaver effects emphasize the landscape-level impacts of beaver activities on streams and riparian zones (e.g. Rémillard et al. 1987, Johnston et al. 1993), studies of regional influences on riparian vegetation rarely mention beavers. This disparity may be due in part to a focus on studying large rivers (where beavers are not building dams, or in areas where beavers have been extirpated or did not naturally occur) or may reflect a general tendency in ecology to underestimate the magnitude and diversity of animal influence on ecosystems (Pollock et al. 1994).

4 KEYSTONES SPECIES

In a seminal 1966 article, Paine introduced the idea of a "keystone species" : one whose removal causes a significant decrease in community species diversity. He was referring to the intertidal sea star *Pisaster ochraceous*, and intertidal rocky shores where *Pisaster* predation on mussels prevents these dominant space competitors from excluding all other species. The term "keystone" was coined in a follow-up 1969 article:

> "[T]he species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time… are determined by their activities and abundances" (Paine 1969).

Since this initial conception, the term keystone species has been applied to many species, at many trophic levels, exerting a great diversity of effects on their communities (see reviews in Mills et al. 1993, Power et al. 1996). Keystone species have been identified in all of the world's major ecosystems, and exerting effects not only through predation but also through competition, mutualism, dispersal, pollination, disease, and by modifying habitats (Power et al. 1996). As with all ecological concepts, keystone species have been subdivided into a variety of categories by different researchers, depending on the type of effect and process by which they exert influence on their community (e.g. Mills et al. 1993). The two over-arching criteria, as conceived by Paine (1969) and subsequent proponents, are: that the organism's presence is crucial in maintaining organisation and diversity of the ecological community; and, implicitly, that the importance of the species is exceptional relative to that of rest of the community (Mills et al. 1993).

Some ecologists have begun to seriously question the utility of the term keystone, both because of ambiguity in its use and definition, and because few studies that report keystone species have actually demonstrated the type of community change necessary to meet these criteria (Mills et al. 1993). Although the primary research supporting the theory is based on systems where a key species has been removed (e.g. Paine's *Pisaster* exclusion experiments, sea otter removal from kelp beds (Power et al. 1996)), the majority of studies proposing keystone species have been descriptive of natural history and merely speculative about the organism's crucial rôle in structuring the community (Mills et al. 1993). Demonstrating that a species is keystone, critics argue, requires manipulative exclusion experiments of the community in question: a research agenda fraught not only with the logistic difficulties of excluding species and determining time for community change, variables affected, and amount of change that is biologically significant, but also philosophical fallacies of *a priori* assumptions of a species' importance.

An increasing body of evidence suggests that keystones are context dependent – their influence may vary in different parts of their range or over time, and may interact at various scales with the system's disturbance regime (Power et al. 1996). In light of the criticisms mentioned above, and the variable influence species may have, Power et al. (1996) suggest a revised definition of a keystone species: "one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance".

This new definition does not, of course, solve the difficulty of the ambiguous nature of the term "keystone" nor address the issue of specified effect criteria and size used to evaluate (preferably, controlled) experiments of species' influence. Mills et al. (1993) suggest that the value of the keystone concept is that it highlights differing strengths of links in food chains; they suggest that to "better serve the pursuit of science", ecologists should drop the dualism of a keystone / nonkeystone mentality, and focus on research that examines interaction strengths within communities, and searches for trends across communities.

Chapter 3 Chronosequence of Sites

> "In the foregoing discussion the beaver flows and beaver meadows have been considered merely as such, and no allusion has been made as to the possibility that neither the one nor the other may be a fixed and permanent feature of the landscape. Yet such is actually the case, and this thought should be a source of some comfort to those to whom the beaver flow of today is a matter of such deep concern: who see in it nothing more than a blot upon the landscape, a peril to deer, a curse to the woods tramper, and even – if one should take some alarmists at all seriously – an ominous forecast of impending doom to the entire Adirondack forest."
>
> Johnson 1927 p 587

1 INTRODUCTION

The boreal forest is described as a 'disturbance ecosystem' (Rowe 1961), and in the past few decades researchers and managers have come to appreciate the complexity of factors determining its vegetation structure and composition (Pojar 1996). Stand-destroying wildfire has long been recognised as a key ecosystem process and considered the dominant disturbance in boreal forests (Pojar 1996), but recent research has highlighted the importance of other disturbances such as insects, windthrow (Pojar 1996), flooding (Helm & Collins 1997), and herbivory (Pastor et al. 1988, Pastor & Naiman 1992). Dynamic disturbance regimes and multi-path succession produce high ecosystem and landscape diversity (Pojar 1996).

Wetlands are a major feature of the landscape in Alberta's boreal mixedwood forests, comprising more than 20% of the landbase (AEP 1994a, Johnson et al. 1995), with this proportion increasing to almost 50% in northeastern portions of the province (Strong 1992). Mosaics of wetlands are the most productive and diverse habitats in this region (Strong 1992). These wetlands, and their riparian areas, are strongly influenced by beaver activity. Beaver dams convert aquatic systems from lotic to lentic, dramatically affecting hydrogeomorphologic characteristics of stream networks (e.g. Naiman et al. 1986, 1988b). Beaver browsing, in conjunction with the effects of flooding and then draining of ponds, creates riparian meadow and shrub patches that may last for decades or longer (e.g. Wilde et al. 1950, Naiman et al. 1988b, Johnston & Naiman

1990c, Chapter 5 this thesis). These beaver-influenced riparian areas contribute significantly to regional diversity of plants (Wright et al. 2002), mammals (Medin & Clary 1991, Collins & Helm 1997), aquatic insects (McDowell & Naiman 1986) and birds, especially waterfowl (Beard 1953, Neff 1957, Nummi 1992, Rempel et al. 1997, McKinstry et al. 2001).

Numerous studies have examined changes over time in individual beaver ponds, and in basin-wide impacts of beaver activity, by analysing time-series of aerial photos (Rémillard et al. 1987, Johnston & Naiman 1990c, Johnston et al. 1993, Meentemeyer & Butler 1995), sometimes in combination with GIS analyses (Johnston & Naiman 1990b, Townsend & Butler 1996, Snodgrass 1997). These studies, and early natural history observations (Warren 1932, Neff 1959), provide a picture of the complex and variable impacts of beaver activities across the landscape. Over time, beaver dam sites may be abandoned, recolonised, and then abandoned again in cycles lasting from decades to centuries (Warren 1932, Neff 1959, Johnston & Naiman 1990c, Meentemeyer & Butler 1995). After a dam is breached and the pond is drained, typically the area is colonised by sedges and grasses, and then by shrubs or trees, the duration of each phase depending, among other factors (Naiman et al. 1988b), on soil type (Wilde et al. 1950) and water table (Terwillegar & Pastor 1999). Although the usual effect of beavers on wetlands themselves seems to be to return them to an earlier successional stage (Johnston & Naiman 1990c, Syphard & Garcia 2001), vegetation changes in the surrounding riparian area are highly variable and, as concluded by Rémillard et al. (1987, p 116), "successional changes in plant communities within beaver patches are non-linear and multidirectional". Hereafter, I refer to this process of dam-building, abandonment, and reoccupation as the "beaver cycle".

The spatial and temporal dynamics of beaver pond distribution appears to be an important feature of boreal landscapes (Johnston & Naiman 1990b), dramatically altering large portions of systems (Johnston & Naiman 1990c, Johnston et al. 1993), with effects that can last for centuries (Ruedemann & Schoonmaker 1938). The cycle of beaver activity leads to successional sequences of wetland types (Syphard & Garcia 2001) and riparian vegetation types (Remillard et al. 1987, Terwillegar & Pastor 1999) that are important for regional survival of fishes (Schlosser & Kallemeyn 2000, Snodgrass &

Meffe 1998), aquatic invertebrates (Clifford et al. 1993), and ungulates (Collins & Helm 1997).

Although recent research is improving our appreciation of beavers' rôle in boreal landscapes, these studies have all been conducted in eastern North America; the impact of beaver activities in boreal mixedwood forests is unknown. The primary objective of this study was to examine spatial and temporal change in beaver dam presence at six study sites, to increase understanding of the beaver cycle in boreal mixedwood forests. A second goal was to examine forest management implications of beaver activity. Riparian areas around wetlands and streams have long been considered 'biodiversity hotspots'. Riparian areas support a different species composition of plants (e.g. Tabacchi et al. 1996, Suzuki et al. 2002), small mammals (e.g. Darveau et al. 2001), birds (e.g. LaRue et al. 1995, Machtans et al. 1996), and amphibians (Mensing et al. 1998) than adjacent upland areas and are thus important for regional biodiversity (Naiman et al. 1993). Riparian areas are also known to protect aquatic biota from negative impacts of upslope industrial activities; for this reason, and the biodiversity values mentioned above, riparian areas are often protected with no-harvest "buffer strips" (Castelle et al. 1994, Naiman et al. 2000b, Lee et al. 2004). Alberta's Forestry Operating Ground Rules call for riparian buffers of 30 to 100 m wide, depending on the type of stream or waterbody (AEP 1994b). In some parts of the boreal forest where there are few upland protected areas, riparian buffers may become the only reserves of old forest stands (post-rotation age) (Darveau et al. 2001; S. Cumming, unpublished data).

Current buffer prescriptions in Alberta do not consider the natural dynamics of riparian vegetation or the surrounding upland areas, and are not based on ecological data from the area. Both ærial photos and field surveys show that beaver activity has a dramatic impact on riparian forests. For example, beaver foraging removes deciduous trees in a wide band (30 – 50 m) surrounding the pond and lodge – thus, riparian areas altered by beavers may not fulfill the management objectives of maintaining intact riparian forest strips and providing residual blocks of mature forest cover. By linking results of an air photo analysis and field surveys of beaver dams (see Chapter 5), I examined potential effects of beavers on buffer strips and implications for forest management policy.

2 METHODS

2.1 Aerial photo chronosequence analysis

I examined a time sequence of 9 – 13 ærial photos for each of my study sites, both paired sites (paired road crossing and active beaver dam on the same stream) and road crossing only (refer to Figure 1.2 for study area and site locations). Each photograph, taken in a different year, represents a time-step in the chronosequence. The photos were taken between 1951 and 2002. The years available for each site varied, and thus the interval between each time-step is also variable among and within sites. There was a photo of every site in years when the full FMA was photographed (1951, 1978) and almost all sites had a photo from 1997 / 98 and 2000 – 02; only site 5 did not have a photo more recent than 1997 (refer to Table A3.1 for full details of photos used). For intervening years, photo availability differed among sites and any photos at 1:30 000 or finer scale were used (Table 3.1). For each photo, I recorded the presence or absence of beaver dams at the study dam (the dam site surveyed in the field study), the presence or absence of a pond at the road-crossing site, the presence of any other dams within 100 m of the road crossing, and general comments about other dams observed along the stream corridor, that is along the stream within approximately 1 km upstream or downstream of the dam. I recorded only dams that had impounded water in the photo examined. For dams without a pond, I could not determine if they had drained because they were abandoned, or because of low water tables; in either case, lack of water would preclude beaver habitation and make it an inactive dam. Dams were usually clearly visible at a scale of 1:20 000 or finer but at 1:30 000 my ability to identify beaver dams and small ponds was dependent on quality of the photo. I defined road age as the year the road was built; for some of the sites, this information is in AlPac's AVI database (Alberta Vegetation Inventory) and for others, I found an approximate age by noting in which year the road first appears in the air photos. For beaver dams, I have based age on the first photo where a pond appears, however, I have no way to assess whether the dam was intact during the intervals between photos (it may have been breached and repaired in the interim) nor how long it had been present before its first appearance.

2.2 Site-level beaver effects

I used vegetation zones and beaver foraging data to examine the mechanisms of riparian change at study sites. For these analyses, I used basal area of *Populus* (aspen and poplar) stumps and trees measured in each plot at each site (reinterpreting data presented in Chapter 5). I used plot as a distance measure and calculated the average basal area of stumps per plot. I also added stump and tree basal area to calculate the total *Populus* basal area per plot, to approximate pre-browse. These were averages across all transects, pooling treatments and sites. Meadow zones were interpreted to have been caused by a combination of flooding and tree-felling due to beavers. I calculated average meadow zone width (perpendicular from water's edge) at each site, averaged across transects, pooling treatments.

Table 3.1 Year and scale of ærial photos used in chronosequence analysis for each site.

Site 4

Year	Scale
1951	1:15 840
1964	1:31 680
1967	1:31 680
1978	1:15 000
1988	1:20 000
1992	1:15 000
1997	1:15 000
2000	1:20 000
2002	1:20 000

Site 5

Year	Scale
1951	1:15 840
1965	1:31 680
1973	1:21 120
1978	1:15 000
1985	1:10 000
1986	1:25 000
1988	1:40 000
1990	1:15 000
1995	1:15 000
1997	1:15 000

Site 7

Year	Scale
1951	1:15 840
1967	1:31 680
1974	1:24 000
1978	1:15 000
1983	1:60 000
1990	1:40 000
1993	1:15 000
1998	1:20 000
2000	1:30 000

Site 9

Year	Scale
1951	1:15 840
1961	1:31 680
1977	1:50 000
1978	1:15 000
1979	1:25 000
1983	1:60 000
1991	1:40 000
1996	1:15 000
2002	1:20 000

Site 12

Year	Scale
1951	1:15 840
1967	1:31 680
1975	1:31 680
1978	1:15 000
1982	1:30 000
1988	1:15 000
1992	1:15 000
1997	1:15 000
2000	1:20 000

Site 13

Year	Scale
1951	1:15 840
1965	1:31 680
1970	1:15 840
1971	1:15 840
1972	1:12 000
1973	1:21 120
1978	1:15 000
1981	1:16 000
1989	1:20 000
1991	1:20 000
1995	1:15 000
2001	1:20 000
2002	1:20 000

Site 14

Year	Scale
1951	1:15 840
1965	1:31 680
1973	1:21 120
1978	1:15 000
1981	1:16 000
1982	1:6 000
1988	1:40 000
1990	1:15 000
1995	1:15 000
1997	1:15 000
2001	1:20 000

Site 15

Year	Scale
1951	1:15 840
1967	1:31 680
1975	1:31 680
1978	1:15 000
1980	1:15 000
1990	1:20 000
1991	1:20 000
1993	1:15 000
1998	1:15 000
1999	1:15 000
2000	1:20 000
2002	1:20 000

Site 16

Year	Scale
1951	1:15 840
1967	1:31 680
1978	1:15 000
1979	1:20 000
1982	1:30 000
1992	1:20 000
1993	1:15 000
1994	1:20 000
1995	1:20 000
1998	1:20 000
2000	1:20 000
2002	1:20 000

3 RESULTS

3.1 Aerial photo chronosequence analysis

Dam ages ranged from 1 year to more than 35 years (Table 3.2). Many of the dams were built in locations where earlier photos had evidence of a previous dam. Several of the stream corridors had sequences of dams built, abandoned, and rebuilt over the 50-year period, in shifting locations along the stream (Figure 3.1).

Table 3.2 Estimated ages of dams used in field study, from air photos

site	year pond appears	pond age (years)	field notes / comments
4	between 1964 and 1967	> 35	dam is recently rebuilt from old breached dam, other fresh dams along stream
5	between 1973 and 1978	> 24	dam is recently rebuilt from old, overgrown, breached dam; pond has a lodge
7	between 1990 and 1993	> 12	series of older dams around site, also fresh dam just downstream
9	2002	< 1	dam new-built, with green leaves still on flooded trees, other new dams just downstream
12	between 1997 and 2000	> 5	dam is very fresh, lots of evidence of past activity all along stream
13	2001	1	dam new-built, with green leaves still on flooded trees, old dams upstream and new one downstream

Figure 3.1 Graphical representation of dam presence at dam site used in field survey, as seen on photos

Site	1951	1961	1964	1965	1967	1970	1971	1972	1973	1974	1975	1977	1978	1979	1981	1982	1983	1985	1986	1988	1989	1990	1991	1992	1993	1995	1996	1997	1998	2000	2001	2002
4	🟩		🟩		🟥								🟥							🟥				🟥			🟥			🟥		🟥
5	🟩			🟩					🟩				🟥					🟥	🟥	🟥		🟥				🟥		🟥				🟥
7	🟩				🟩					🟩			🟩				🟩					🟩			🟥				🟥	🟥		🟥
9	🟩	🟩										🟩	🟩	🟩													🟩					🟥
12	🟩												🟥			🟩				🟩				🟩				🟩		🟥		🟥
13	🟩			🟩		🟩	🟩	🟩	🟩				🟩		🟩						🟩		🟩			🟩					🟥	🟥

🟩 no dam at site in photo

🟥 dam at site in photo (or in field for 2002)

A blank space indicates no photo available.

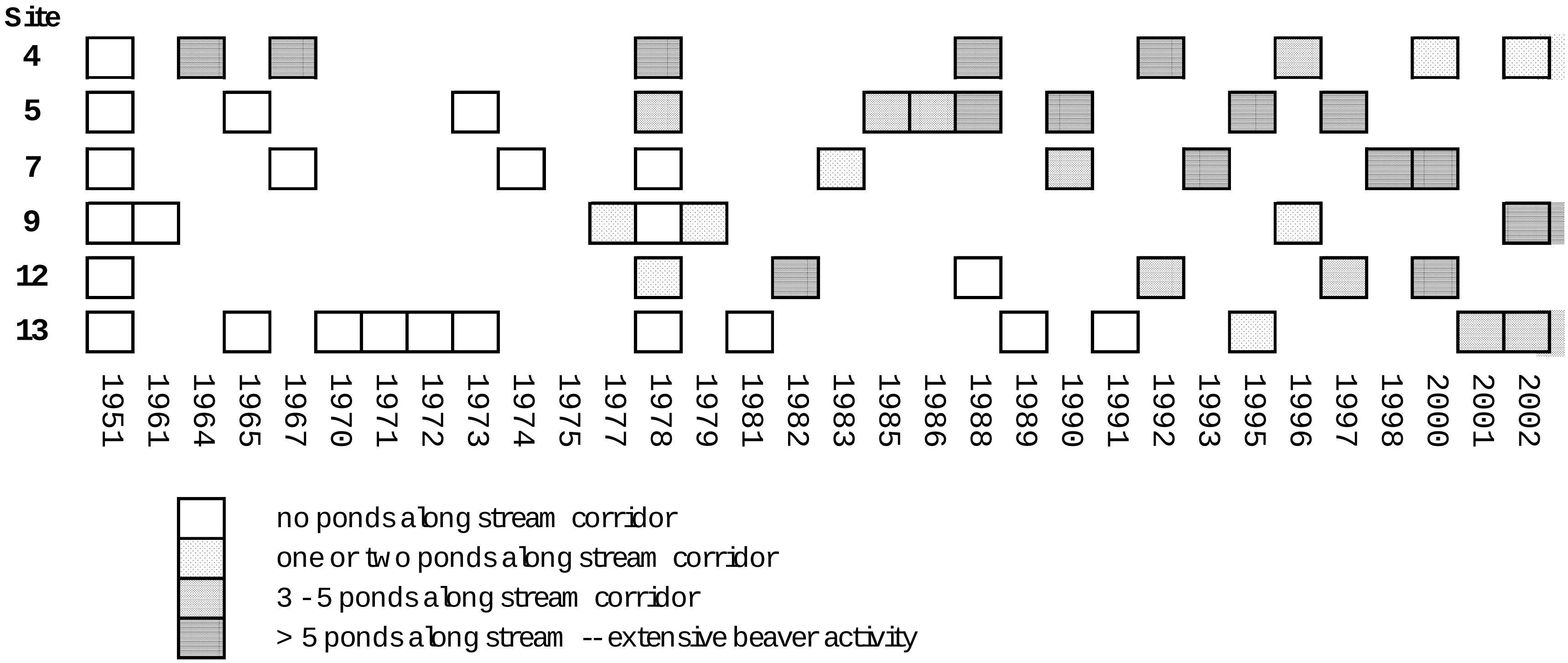
Overall, the sites showed dramatic changes in riparian areas and surface water over time. In 1951, almost no dams or ponds were present and the streams and riparian areas were narrow and almost indistinguishable from the surrounding forest. In about the mid-1970's, beaver dams started to appear, increasing in abundance through the '80's, and by the early '90's large sections of these streams had been converted to lentic habitats. The extent of beaver activity varied among sites but all sites showed increasing dam abundance over time (Figure 3.2). Meadows and shrub areas from drained ponds significantly increased the diversity and width of riparian habitats (Figure 3.3). The consecutive drought years of 2000 - 2002 had dewatered most ponds by the time of the most recent photos and the field survey (conducted 2002).

Road ages ranged from at least 35 years to no more than 9 years (Table 3.3). The road-only sites (14, 15, 16) all had evidence of beaver activity along the creek, but these ponds were dry at the time of field study due to drought. Upstream impoundments at road crossings were infrequent, short-lived, and generally very small (that is, ponds immediately upstream and likely to have been caused by beaver plugging the culvert or building in very close proximity to the road crossing).

Data on dam dynamics at each site varied, and are presented individually.

Figure 3.2 Intensity of beaver activity along stream corridor as evidenced by ærial photo analysis.

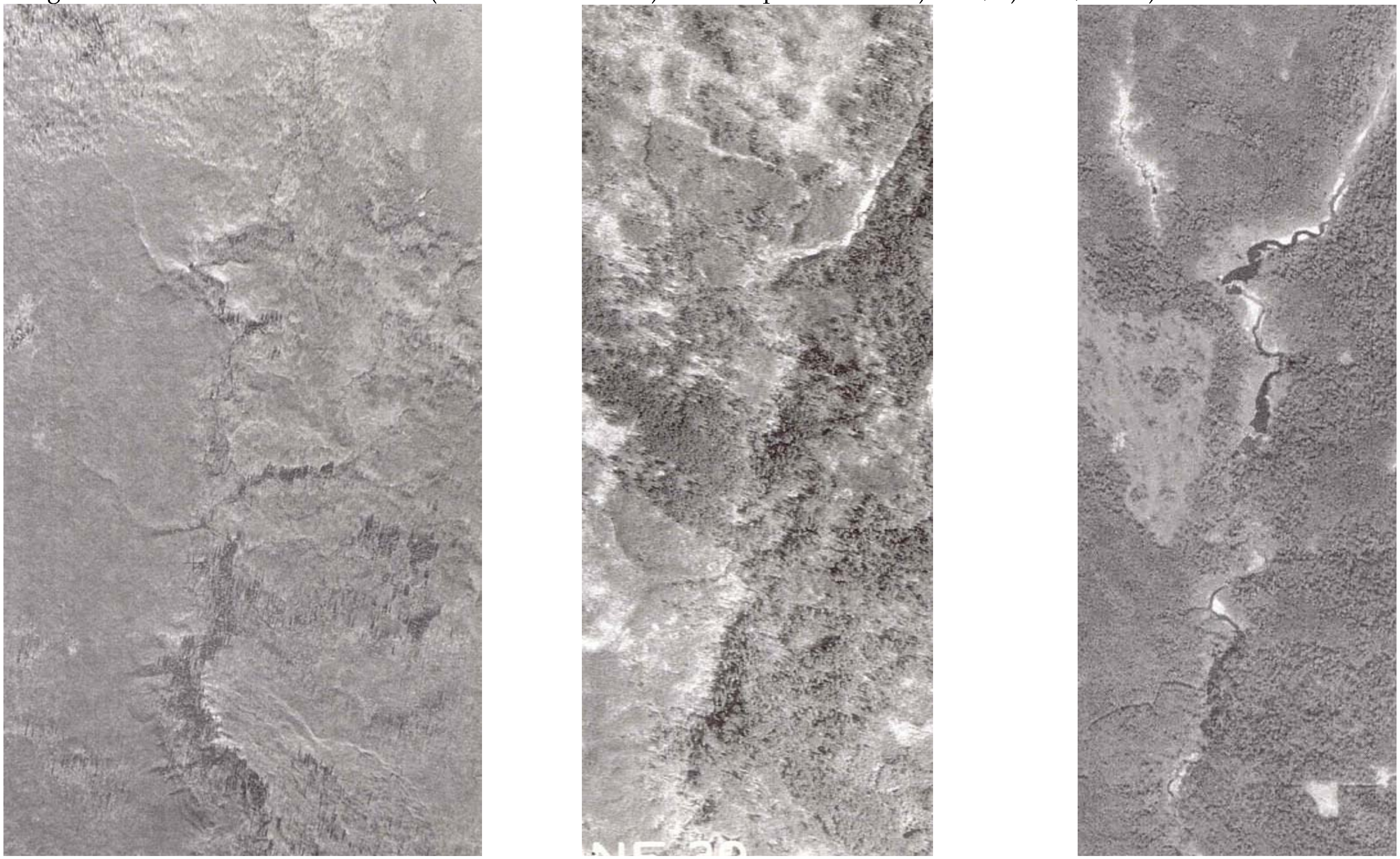
Stream corridor consists of approximately 100 m downstream of the road crossing and 700 m upstream. Only dams with impounded water upstream were considered 'active' and included in the analysis.



A blank space indicates no photo available.

Figure 3.3 Air photo sequence showing riparian change with increasing beaver activity along stream corridor

Images are the same stretch of stream (a stream near site 4) in aerial photos from a) 1951, b) 1978, and c) 2002



a) 1951 b) 1978 c)2002

Table 3.3 Estimates of Road Age

site	year road constructed*	road age (years)
4	1959	43
5	1987	15
7	between 1993 and 1998	9 max
9	1980	22
12	between 1951 and 1967	34 min
13	1972	30
14	1987	15
15	between 1967 and 1975	25 max
16	1992	10

3.1.1 Site 4

This site had evidence of more than 30 years of shifting beaver activity (Appendix 3.2). The study dam at this site appears in every photo since 1967 and was at least 35 years old at the time of field survey. There were no visible beaver dams on any streams in the area in 1951 but there have been dams on this stream since at least 1964. The study dam, and others along the stream within a few hundred metres, drained and were rebuilt periodically through the 50-year period studied. In 1997, many of the ponds visible in the previous photos (visible from 1970's onward) were drained, and by 2000, the area was almost completely dry with very wide meadows around the stream where ponds had been.

The road was constructed in 1959, and was the oldest road studied. A pond upstream of the road crossing was visible in 3 of the time steps.

3.1.2 Site 5

The study dam on this stream appears in the 1978 photo, and thus was at least 24 years old during the field survey. It seems to have been rebuilt from an old, drained dam visible in the 1951 photo and our field survey showed sections had been repaired recently. In the 1951 photo, there are no ponds visible on any of the area's streams although there are conspicuous old, drained dams, indicating beaver had been active in the area previously. The study dam and pond grew until the most recent photo in 1997, and a series of dams were built downstream during the 1980's and '90's. (Appendix 3.3). These downstream dams had drained at the time of field survey.

The road at this site was constructed in 1987, and was 15 years old during the field survey. There are several dams downstream of the road crossing between 1986 and 1990, and an impoundment at the road crossing in 1997. There are no photos available after 1997 for this site.

3.1.3 Site 7

The study dam at this site appears definitely in the 1993 photo (possibly in 1990) and was therefore at least 9 years old in 2002. At this site, the 1951 photo showed old, overgrown dams but no active dams (with a pond) (Appendix 3.4). Active dams did not appear until 1983 although a few may have been present in the 1978 photo (heavy shadows made it difficult to see the stream). A chain of dams, some of them new and some rebuilt from the old (pre-1951) drained dams, was built between 1978 and 1998, and in 1998 there was a series of large ponds up and down of the study dam. In the 2000 photo, most of these ponds were drained and wide meadow zones were visible along the stream.

The road at this site was constructed between 1993 and 1998, and is a maximum of 9 years old. In 1998, an impoundment is visible upstream of the road crossing.

3.1.4 Site 9

At this site the study dam was very fresh, less than 1 year old based on green leaves on flooded trees during the field visit in 2002. This site was quite hard to see on the air photos and few were available at an appropriate scale. In 1959, there were several dams about 1 km upstream, but dams were not built closer to the study dam location until 1977 (Appendix 3.5).

The road at this site was constructed in 1980. There was a small impoundment at the road in 2002.

3.1.5 Site 12

The study dam at this site is fairly new, no more than 5 years old. On this stream, ponds did not appear until 1978 (Appendix 3.6) and then over time numerous dams appear and disappear along the stream upstream of the road crossing site. A chain of large ponds was visible in 1992. The 2000 photo shows most of the ponds visible in earlier photos had drained, and had wide meadow zones.

The road at this site was constructed between 1951 and 1967.

3.1.6 Site 13

The study dam was very fresh (no more than 1 year old), and although there were dams about 600 m further upstream, there were few dams in the immediate vicinity of the study dam location during the air photo sequence. This site had very little evidence of beaver activity in the 50-year study period (Appendix 3.7).

The road was built in 1972.

3.1.7 Site 14 (road only)

This site showed very little beaver activity (Appendix 3.8) although in the field survey we found numerous small, breached dams upstream of the road crossing. Several dams were visible in the 1978 photo and through the 1990’s, but these ponds were drained at the time of the field visit in 2002 (some are still present in the 2001 photo).

The road was built in 1987. In the 2001 photo, there is a pond upstream at the road crossing.

3.1.8 Site 15 (road only)

This site had signs of beaver activity from the late 1970’s (Appendix 3.9). A series of dams upstream of the road crossing appears in the 1978 photo, the ponds grew larger in the 1980’s, but then began to drain in the ’90’s and are gone by the 2000 photo. There is a large pond about 200 m upstream of the road, whose dam first appeared in the 1980 photo, and although the pond is present in the 2002 air photo, it had drained by the time of the field visit 2 months later.

The road was built between 1967 and 1975.

3.1.9 Site 16 (road only)

Dams appeared near site 16 in 1992, but these ponds had drained out by 1998, as had the few downstream dams that were built in the early '90's (Appendix 3.10).

The road was built in 1992.

3.2 Site-level beaver effects

The oldest sites had wide meadow zones surrounding ponds and dams, created by a combination of beaver flooding and foraging (Table 3.4).

Table 3.4 Dam age and average meadow zone width (m) at surveyed beaver dams.

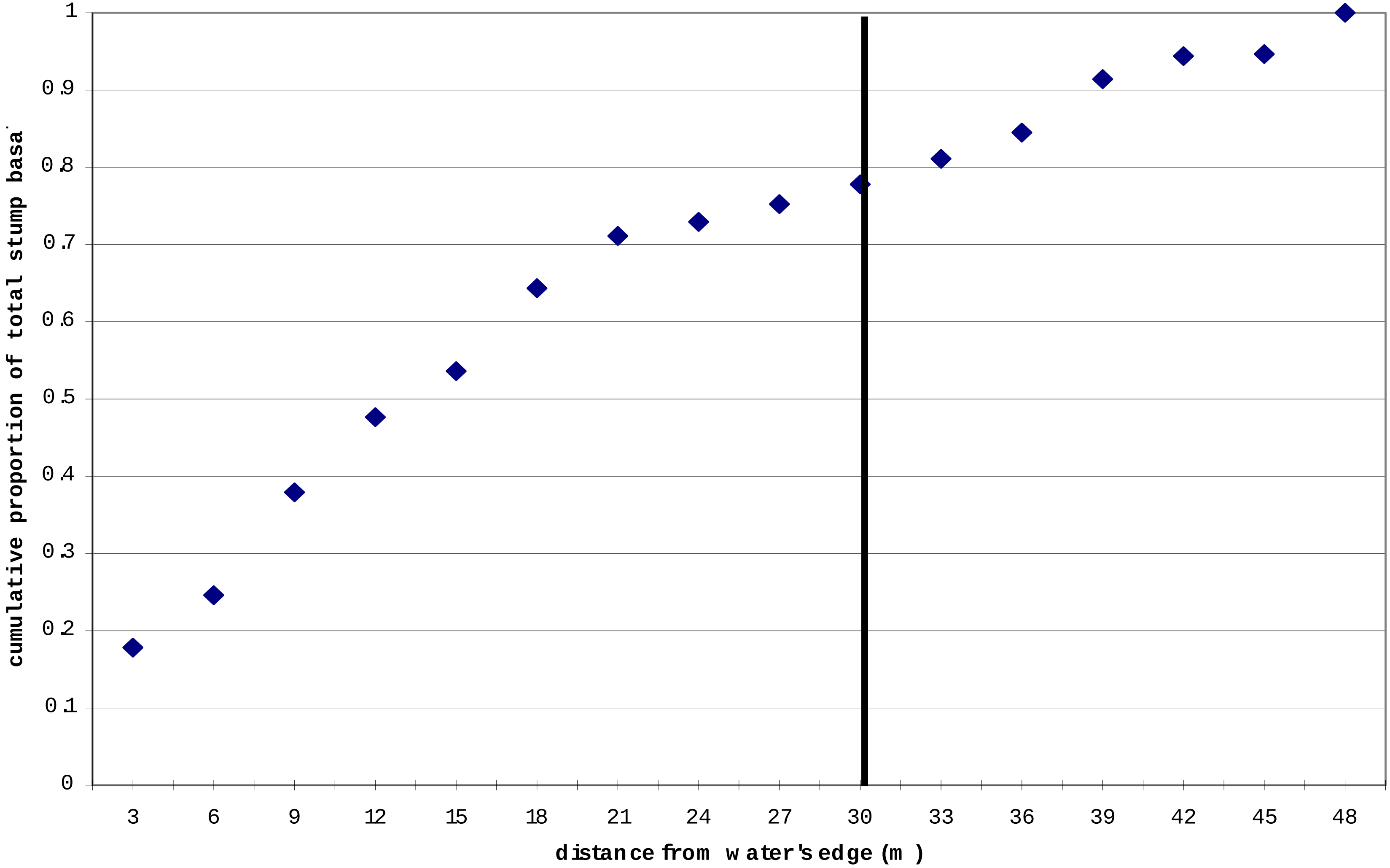
Site	Dam age (year)	Meadow Zone Width (m)
4	35	24.5
5	24	20
7	9	7.5
9	1	1.5
12	5	15
13	1	5

1 Dam ages were estimated from year of first appearance of a pond in the aerial photos.

2 Width represents distance from water's edge to upland edge of each vegetation zone, averaged across transects at each site. Zones were defined using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges. Zones were delineated for each plot surveyed (3 x 3 m); here they have been converted to approximate m for ease of interpretation.

The proportion of total available *Populus* felled by beavers decreased with distance from water's edge (Figure 3.4). At 30 m from water's edge, beavers have removed on average 77.8% of the total amount they would forage from the site.

Figure 3.4 Relationship between cumulative proportion of total *Populus* cut, and distance from water's edge. Plot was used as a distance measure. Data are (cumulative stump basal area up to distance x / total stump basal area at site). The heavy line at 30 m distance from water's edge represents the Alberta OGR riparian buffer requirement for these streams.

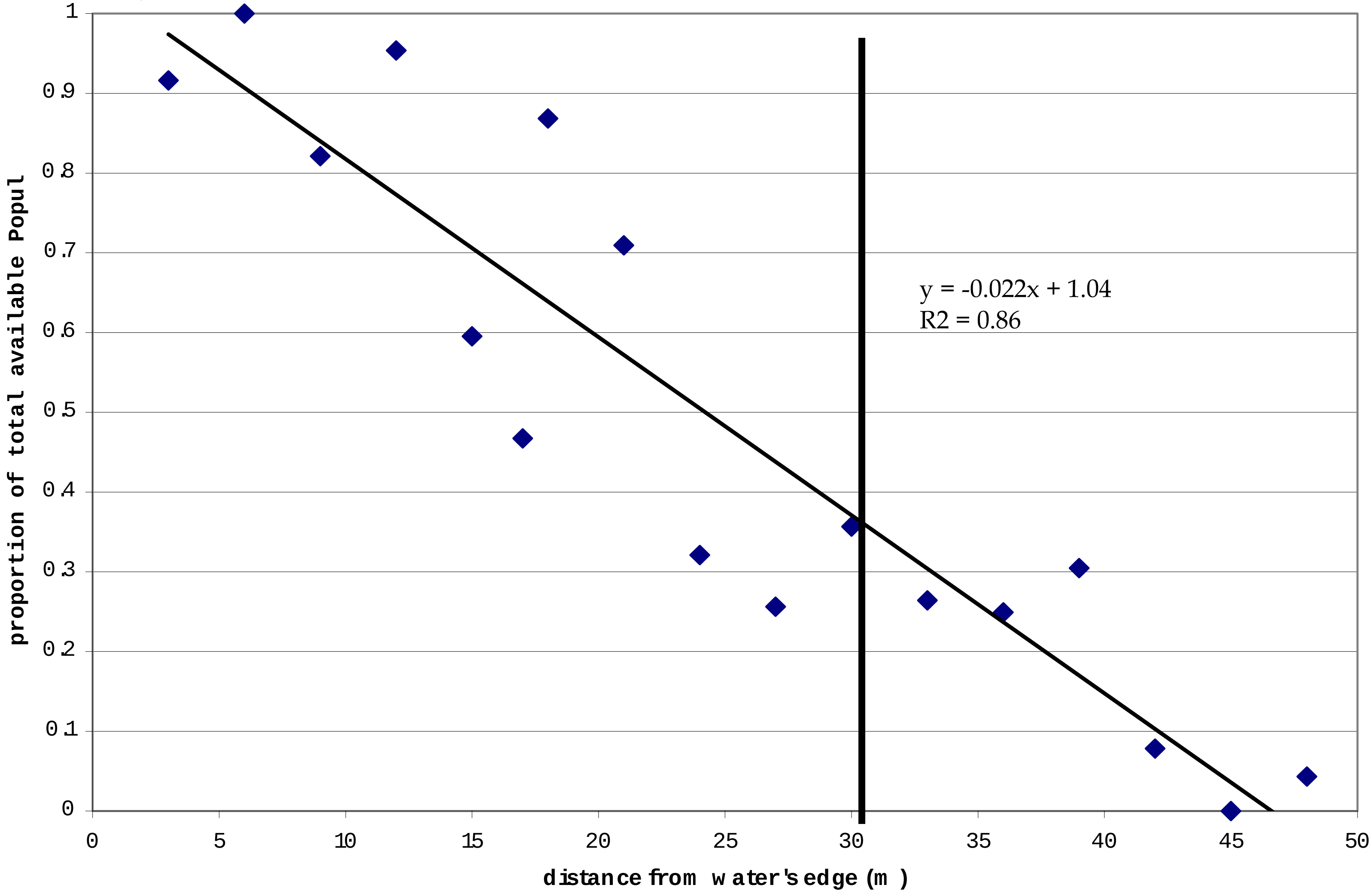


Beavers used a decreasing proportion of available *Populus* with distance (Figure 3.5). The linear regression equation for this relationship was calculated as:

proportion of available basal area cut at distance $x = -0.0223(x) + 1.0412$

The area under this line represents the proportion of *Populus* trees that have been cut. At a distance of 30 m from water's edge, 71.2% of all available *Populus* basal area had been harvested by beavers.

Figure 3.5 Relationship between *Populus* foraging intensity and distance from water's edge. Plot was used as a distance measure. Data are (stump basal area in plot / stump + tree *Populus* basal area in plot). The heavy line at 30 m distance from water's edge represents the Alberta OGR riparian buffer requirement for these streams.



4 DISCUSSION

It is important to remember that the ærial photo interpretation data are my professional judgement, based on variable image quality, and not a detailed study of dam site location and longevity. Despite these limitations, however, I am confident of the general trends observed in the aerial photo sequence at the sites.

4.1 Beaver Impacts on Riparian Vegetation

Two general patterns emerge from this study: the extreme variability of beaver use and impact across the landscape, and the dramatic changes to streams and riparian areas with increasing beaver activity.

Very few of the 1951 air photos showed any active beaver ponds although 1/3 of them showed unmistakable remains of older, breached dams. Over the 50-year study period, the number of visible beaver dams increased considerably. This increase in beaver presence is presumably due to population recovery after previous severe decline. By the late 19th Century, trapping pressure had extirpated the beaver from much of its former range in North America. This near-extinction of beavers was followed by trapping controls (largely through price reductions in the fur market) and reintroduction programmes (Müller-Schwarze & Sun 2003). With reduced trapping pressure, beaver populations can recover quickly from extirpation (Johnson 1927, Johnston & Naiman 1990c, Müller-Schwarze & Sun 2003) and can recolonise rapidly after reintroduction (Fustec et al. 2001). Where beaver populations are stable, there is little fluctuation of dam abundance across the landscape (Meentemeyer & Butler 1995).

The number of ponds increased over time through both rebuilding a breached or abandoned dam and creation of new dams. Although dams were often abandoned and then rebuilt throughout the study period, for the most part dam locations were fairly constant; that is, previously abandoned sites were recolonised by repairing existing dams rather than constructing new ones. At one site (site 5), remnant dams that are visible in the 1951 photo were rebuilt in the 1970's, highlighting the longevity of beaver dams as a geomorphic agent (as also discussed by Ruedemann & Schoonmaker 1938). Other researchers have reported a similar fidelity of dam location through each phase of reoccupation and abandonment (Neff 1959, Meentemeyer & Butler 1995). The overall number of dams also increased over time. Typically, new dams were built in close proximity to existing dams rather than being built in isolated locations along the stream corridor. Individual ponds thus became chains of ponds connected by a sequence of dams, and beaver ponds became less isolated on the landscape (as also reported by Townsend & Butler 1996).

As the number of beaver dams along the study streams increased over time, channel morphology of some of the study streams was altered dramatically. Beaver dams created ponds interspersed along the stream, converting narrow, entirely lentic habitats to a mixture of lentic and lotic habitats. Dam abandonment and draining widened the riparian area and generated patches of meadow, shrub, and early-successional forest along the stream corridor (see also Chapter 5). These findings are consistent with reports from other areas with recovering beaver populations. In a recent study in Wyoming, the riparian width in streams with beaver ponds was more than three times the riparian width in similar streams without beavers (McKinstry et al. 2001). In New York State, over 45 years of population recovery, beavers increased the area of aquatic habitat by 43%, and converted the study area from a landscape dominated by forest to a spatial mosaic of aquatic and terrestrial habitats (Johnston et al. 1993).

A second striking feature of the streams studied here is the extreme among-site variability of dam abundance, pond longevity, and beaver impact. Ponds at some sites were quite stable. At other sites, ponds went through the cycle of building, draining, and rebuilding several times throughout the 50-year air photo record. The apparent influence of beavers, in terms of altering channel morphology and riparian habitat availability, also varied among sites, evidently correlated with time since first occupation. Presumably, differences in availability of food and construction material, topography, and beaver demographic factors also contribute to among site variation.

4.2 Beaver Cycle

Conventional wisdom holds that beavers leave an area after they have depleted the food resources, and return once preferred species are sufficiently available. Few researchers have explicitly studied causes of abandonment. With two exceptions (Fryxell

2001, Meentemeyer & Butler 1995), all time-series analyses of beaver effects have occurred in areas and times of expanding beaver population. Even though these studies describe dam abandonment, they do not report forest regrowth, and only Neff (1959) reports site reoccupation. It would seem, therefore, that although ecologists describe an occupation → abandonment → reoccupation cycle, we are not currently seeing all of these phases. One explanation is that beavers have not saturated available habitat in these areas: beavers are able to find unexploited stream reaches rather than reoccupying old sites. It may also be that the 50 years for which we have an aerial photo record is simply too short a time-frame to allow for sufficient vegetation regrowth to support beaver colonies.

4.3 Implications for Forest Management: Buffer Strips

Much of our understanding of how streams and riparian areas function is based on studies of systems that already have been altered by beaver removal through near-extirpation. Based on the extent of beaver influence revealed in this study, beaver extirpation may have altered the boreal mixedwood landscape dramatically.

Alberta's forestry Operating Ground Rules (OGR) require unharvested buffer strips to be left adjacent to water bodies (AEP 1994b). For the small streams in this study, a 30 m buffer would be required on either side (currently, there are no provincial guidelines for wetlands or flooded areas). The expressed goals of Alberta's buffer strip requirements are to "minimize the impacts of harvest operations on water yield, regime and quality, watercourse structure, soils, cover and riparian habitat for fish and wildlife" (AEP 1994b). Based on my study results, buffer strip regulations that do not consider beaver activity may not achieve these objectives.

First, from a beaver's perspective, a 30 m buffer may not provide sufficient long-term forage for dam- and lodge-building and feeding requirements. In a pilot study, I found that almost all beaver foraging occurs within 50 m of water's edge in the boreal mixedwood, and is practically non-existent beyond 60 m. At my sites, approximately 75% of beaver foraging by volume occurred within 30 m of water's edge. The beaver dams in this study had created ponds on average 15 - 20 m wide on each side of the stream – thus, a pond near a cutblock would flood most of the buffer strip and leave the beavers with few large trees for construction materials. A 30 m buffer strip may therefore be insufficient to accommodate beaver habitat needs.

Second, Alberta's buffer requirements might be inadequate from the perspective of protecting water quality and providing riparian habitat for other wildlife since the wide flooded and foraged zones created by beavers may eliminate entire buffer strips (see also Chapter 5). Within the 30 m buffer strip, on average 71% of available *Populus* basal area was removed by beavers, and at older sites this proportion rose to 100%.

Alberta's forestry Operating Ground Rules were developed without using local ecological data, and without consideration of disturbances within riparian zones. The results of this study challenge the buffer widths prescribed in the current OGR's and indicate that they are inadequate to achieve the OGR's expressed management goals. Wider buffer strips could accommodate pond creation, while still retaining some surrounding forest structure for both beaver forage, and protecting aquatic systems from impacts of upland harvesting.

4.4 Recommendations

While buffer strip requirements in boreal areas are wider, on average, than in other parts of North America (Lee et al. 2004), very little is known about riparian habitat function in northeastern Alberta. There have been few evaluations of wildlife use of riparian areas in boreal mixedwood forests, and even fewer of how successfully buffer strips conserve species and ecological processes (Stelfox 1995, but see Machtans et al. 1996, Hannon et al. 2002 for two recent studies). A critical first step to improving our understanding and thus management policies for riparian areas should be preliminary studies of riparian habitat use. It is also imperative to study the effectiveness of buffers of different widths for achieving the expressed management goals of maintaining habitat availability and protecting water quality.

This study's results highlight the influence of beaver activity at the scale of a several-kilometre stretch of stream. These sites were known to have beaver activity, since they were chosen based on objectives of other parts of the project, and may not be an accurate picture of beaver effects across a broader landscape. Further studies should quantify the extent and nature of beaver impacts on a watershed scale, and examine how beaver activity varies within watersheds. Comparative studies of beaver-influenced to non-beaver-influenced areas would elucidate the proportion of landbase affected by beavers, and their relative impacts in different areas (e.g. beaver use of streams in different areas of a catchment, or a different order). A portion of these questions is being addressed by corollary studies at the University of Alberta.

From a beaver's perspective, habitat use may be affected by harvesting activities in the surrounding forest and along the stream corridor. For example, forest harvesting may change the availability of forage trees not only by removing mature aspen and poplar but also by creating patches of regenerating trees. Ten to fifteen years post-harvest, dense stands of aspen suckers on these cutblocks may be particularly appealing to beavers by providing a preferred size-class for both feeding and dam construction. My study sites were chosen to avoid nearby cutblocks. One critical line of enquiry for buffer planning would be an understanding of beaver use of cutblocks near water's edge and specifically of buffer strips themselves: If there is a cutblock with a conventional 30 m buffer strip, do beavers fell these trees as in other areas – or do they bypass these trees in favour of the adjacent regenerating cutblock? How is this use affected by relative landscape availability of intact riparian areas, buffer strips, and cutblocks? These questions could be answered by studying streams harvested using an experimental series of variable-width buffers.

Chapter 4 Road Crossings as Beaver Dam Analogues:

Impacts on Hydrology, Riparian Vegetation, & Beaver Habitat Use

1 INTRODUCTION

Alberta's northern boreal forests have undergone dramatic changes in the last several decades as the region's forest and fossil fuel resources are extracted at an increasing, and astonishing, rate (Stelfox 1995, AEP 1998, Schneider 2002, Schneider et al. 2003). Networks of permanent and temporary roads and other infrastructure accompany this development.

Roads affect a much greater proportion of the landscape than is indicated by their area alone (Reed et al. 1996, Forman & Deblinger 2000, McGarigal et al. 2001), and their impacts can persist on the landscape long after deactivation (road removal) (Trombulak & Frissell 2000), sometimes for centuries (Detwyler 1971, Hutchinson 1973)[1]. The effects of roads range from direct physical impacts (such as geomorphic and hydrologic changes), to landscape level changes (effects on connectivity, animal mortality, and biodiversity), to socio-economic effects (Gucinski et al. 2001). In industrial landscapes of North America, roads have had a much greater impact on forest structure and integrity than logging itself (Tinker et al. 1998, McGarigal et al. 2001). For these reasons, McGarigal et al. (2001) postulate that roads act as a 'keystone landscape element'. Paine (1969) coined the term 'keystone species' to refer to a marine intertidal predator (a *Pisaster* sea star) whose removal results in significant changes to the entire plant and animal community. Since that time, the concept of keystone species has expanded to refer to species whose contribution to ecosystem functioning is unique, whose effect on community structure and ecosystem functioning is disproportionate to their abundance.

In boreal systems of eastern North America, beavers are considered a keystone species structuring wetland and riparian communities across the landscape (e.g. Naiman

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[1] In one striking example, Detwyler (1971) reports enduring effects of roads built during the Roman Empire: limestone slabs, quarried elsewhere, were used to build roads, and even today strips of unique vegetation grow on soils derived from this limestone.

et al. 1988b, Johnson et al. 1993). Through the cycle of dam formation, abandonment, and recolonisation, beavers create a dynamic mosaic of wetland and riparian patches. The complex effects of shifting dam location and beaver foraging intensity are reflected in patterns of wetland abundance that can persist for decades or even centuries (Ruedemann & Schoonmaker 1938, Neff 1959, Johnson et al. 1993). This mosaic of differing ages and types of wetlands is critical for maintaining a diverse community of wetland-dependent wildlife (Gibbs 2000, Schlosser & Kallemeyn 2000).

The extensive road networks being built in northern Alberta may be altering aquatic ecosystems such that they can be considered a ‘keystone process’. Aerial photos of northern Alberta seem to indicate wide road-effect zones at stream crossings, with a “wet-up” effect upstream and a “dry-up” zone downstream, often with upstream water impoundments. These observations have led some managers and ecologists to consider how these aquatic interruptions compare to natural disruptions of stream flow and wetland dynamics.

Jeglum (1975) described road ‘damming’ of flow in slowly drained peatland valleys in northern Ontario, and postulated that “changes caused by the road damming are similar to those caused by beaver dams in that there are increased water tables behind the dam, and slightly drier conditions below it” (p 411). Several researchers have reported a similar phenomenon associated with roads and pipelines built through forested wetlands (Stoeckeler 1965, Boelter & Close 1974). In mountainous areas, roads built into hillslopes can capture and re-route run-off (Wemple et al. 1996, Jones et al. 2000) and intercept sub-surface flow, converting it to surface flow (Megahan 1972, 1983). Roads sometimes redistribute soil moisture throughout drainage basins, creating drier areas below and localized saturated areas above a road (Bowling & Lettenmaier 1997). Few studies in the primary literature have described the effects of road crossings on streams beyond measurements of sediment dynamics or stream flow before and after road construction (Gucinski et al. 2001). The effects of industrial roads have been studied extensively only in mountainous areas. In contrast, the boreal plains of northeastern Alberta have little topographic relief and contain extensive wetland complexes (AEP 1994a). Very little road research has been conducted in low-topography landscapes, or in areas dominated by wetlands.

This study examined the question, *Do road crossings at defined streams function as a human analogue of beaver dams in the boreal mixedwood forest of northern Alberta?* My premise was that altered water tables would be reflected in changes to riparian vegetation structure and composition at road crossings and active beaver dams. I therefore compared upstream and downstream riparian vegetation communities at paired road crossings and active beaver dams and pursued two main lines of enquiry under this general question.

1) *Do road crossings interrupt flow and cause raised water tables upstream of the crossing and lowered water tables downstream?*

At beaver dams, changes to surface and subsurface flow lead to tree death upstream due to flooding, and increased tree growth downstream due to lowered water tables (Wilde et al. 1950). Several researchers have reported similar effects where roads and pipelines cross through forested wetlands and peatlands in Ontario. The consistently higher upslope water table resulted in greater densities of snags compared to downslope areas, reflecting tree death due to saturated soils (Stoeckeler 1965, Boelter & Close 1974, Jeglum 1975). The concomitant lower water levels downslope increased the growth rate of trees below the road (Boelter & Close 1974, Jeglum 1975). These studies also reported changes to upslope riparian composition over time, to communities dominated by plants that can tolerate saturated soils. I predicted similar effects at road crossings in northeastern Alberta. I also postulated that changing water tables would alter relative sapling densities, since saplings of some species experience increased survivorship and growth following changes in soil moisture, while others have decreased survivorship (Green 1947, Hosner 1960). In general, *Populus* spp. and black spruce (*Picea mariana*) can tolerate flooded roots where white spruce (*P. glauca*) cannot.

My hypothesis and its predicted consequences were:

Hypothesis 1: Road crossings at defined streams raise upstream water tables and lower downstream water tables.

Predictions:

1a) greater relative abundance of snags upstream, from tree death due to raised water tables;
1b) larger average tree size downstream, from increased growth due to lowered water levels;
1c) wider upstream non-forest riparian zones (i.e. sedge, grass, and shrub zones) due to the greater tolerance of these plants to saturated soils; and,
1d) deciduous / coniferous sapling ratio greater upstream.

2) *How do effects at road crossings compare to effects at beaver dams*?

Unmaintained beaver dams can remain intact for decades (Neff 1959) and their effects can last even longer (Ruedemann & Schoonmaker 1938, Wilde et al. 1950), however, they are still transient. Roads, conversely, are essentially permanent features: many of their ecological effects, including hydrologic changes, persist long after deactivation (Forman & Alexander 1998, Tague & Band 2001). Roads may therefore form more permanent flow interruptions than beaver dams. If this is the case, roads should exhibit a relatively greater upstream / downstream differences than beaver dams as the effects accumulate over time. Thus, road crossings would have more snags and wider non-forest vegetation zones upstream than do beaver dams.

My hypothesis and its predicted consequences were:

Hypothesis 2: Road crossings are permanent hydrological interruptions; their effects are greater than at beaver dams.

Predictions:

2a) greater number of snags upstream than at beaver dams;

2b) wider upstream meadow zones than at beaver dams; and

2c) difference between upstream / downstream meadow zone width greater at road crossings than at beaver dams.

2d) deciduous / coniferous sapling ratio greater upstream at road crossings than at beaver dams.

Preliminary fieldwork indicated that road crossings and beaver dams are inextricably linked: beavers had dammed virtually every road crossing I examined. It was practically impossible to find road crossing sites that had not been dammed by beavers either currently or in the recent past. Beaver use of road crossings confounded my ability to detect independent road effects. This prompted a new question: *Do road crossings become essentially permanent beaver dams?* Since road crossings are relatively permanent features, beaver use of the surrounding habitat may be essentially continuous. Riparian forests at road crossings would therefore experience more browsing as herbivory effects accumulate through time.

Hypothesis 3: Road crossings are permanent beaver dam sites, concentrating beaver foraging and dam-building activity.

Predictions:

3a) greater numbers of stumps at road crossings compared to beaver dams; and,

3b) greater proportional use of *Populus* at road crossings compared to beaver dams.

2 STUDY AREA AND METHODS

I conducted this study in AlPac's FMA in northeastern Alberta. Descriptions of the study area, study site selection, and field techniques are provided in Chapter 1. The analyses in this chapter are divided into two parts: the effects of roads alone (n=9), and paired comparisons of road crossings and beaver dams (n=6). In all cases, the "treatment" is upstream or downstream location at dams or road crossings.

In all analyses, I used statistical tests that accounted for the extreme variability among sites (e.g. Wilcoxon paired signed-ranks tests, split-plot ANOVA designs). Due to the small sample size, non-parametric tests were used for all analyses. Numerous studies have shown that even when all statistical assumptions are met, the power advantages of parametric tests are small. In situations of unknown or non-normal distributions, non-parametric tests are often vastly more powerful than their parametric counterparts, particularly with small sample sizes (Blair & Higgins 1980, 1985, Sawilowsky & Blair 1992).

At several sites, one transect of the six was missing. Therefore, snag and sapling counts were standardised as densities (counts per 100m^2), using the total count per treatment or per site (i.e. pooled across transects). A summary of variables and transformations used in the analyses is presented in Table 4.1. Each plot along the transects was designated as representing meadow, shrub, or forest vegetation community (see Chapter 1 for details). These different riparian community zones were hypothesised to have been structured by beaver activity – raised water tables and tree-felling create a sedge and grass meadow zone immediately adjacent to water's edge.

Name	**Description**
snag density	number of snags / 100 m^2
proportion upstream snags	ratio of snag density upstream : total snag density
vegetation zone width	average number of plots in each zone type (meadow, shrub, forest)
nonforest zone	meadow zone + shrub zone
tree size	basal area in m^2
sapling density	number of saplings / 100 m^2
proportion deciduous saplings	ratio of density deciduous : density all species
stump density	number of stumps / 100 m^2 for *Populus* (aspen and poplar)
proportion of stump b.a.	ratio of stump basal area : (basal area stumps + trees of *Populus)*

Transformations used

	roads only analyses
Populus snag density	log (snag density + 0.03)^
meadow zone width	log (no. plots + 0.5)
conifer sapling density	log (sapling density)
	roads vs beaver dam analyses
meadow zone width	log (no. plots + 0.3)
nonforest zone width	log (no. plots)
stump density	log (stump density + 0.5)
meadow zone width	rank transformed
nonforest zone width	rank transformed

^ added 1/2 of smallest non-zero value

Table 4.1 Summary of response variables.

2.1 Statistical Analyses for Road Crossings

For analyses of road crossings alone, I used a set of nine widely distributed road crossing sites (Figure 1.2). Basic site descriptions are given in Table 1.2, and Appendices 1.1, 1.2, and 1.3.

Prediction 1a: I compared snag density (snags per 100m^2) per treatment using a total count per treatment at each site, i.e. pooling across transects. A Wilcoxon signed-ranks test was used to test differences in snag density per treatment for all species combined, and for *Populus* snags (*P. tremuloides* and *P. balsamifera* combined). The Wilcoxon signed-ranks test is a non-parametric test that compares the ranks of pairs of values (analogous to a parametric paired t-test). I used Wilcoxon signed-ranks tests to account for differences in forest composition at the different sites. *Populus* snag densities were log-transformed to stabilise among site variance.

Prediction 1b: I compared mean tree basal areas per treatment using a Wilcoxon signed-ranks test (mean for all trees in each treatment at each site). I used data only for the most common tree species (*Populus*, *Picea* (spruce), *Pinus* (pine), and *Abies* (balsam fir)) and compared per treatment average basal area for *Populus*, *Picea*, and all species combined.

Prediction 1c: Vegetation zone width was calculated as the number of plots in each vegetation type, averaged across transects in each treatment. I used a Wilcoxon signed-ranks test to test the hypothesis of differences in average vegetation zone width per treatment. Average meadow zones data were log-transformed to stabilise among site variance.

Prediction 1d: I used the per treatment sapling density (saplings / 100m^2) at each site. The '*Populus*' category consisted of saplings of both trembling aspen (*P. tremuloides*) and balsam poplar (*P. balsamifera*). The 'deciduous' category included both *Populus* and paper birch (*Betula papyrifera*); the 'conifer' category counts all saplings of spruce, pine, and balsam fir. Comparisons involving conifer saplings were made using only those sites supporting mature conifer trees as a seed source (sites 5, 9, 13, 14, and 16; site 12 was also included in the analyses as there were spruce saplings even though no spruce trees were measured). I tested for differences in per treatment sapling densities for each category using Wilcoxon signed-ranks tests. To compare relative proportions of deciduous and conifer saplings I used the ratio of deciduous : total sapling density. Data for conifer saplings were log transformed to correct heteroscedasticity.

2.2 Statistical Analyses Comparing Road Crossings & Beaver Dams

For analyses comparing road crossings and beaver dams, I used data from six paired sites (Figure 1.2). Each site consisted of a road crossing paired with an active beaver dam < 700 m upstream on the same stream. Here, "treatment" is upstream or downstream of the road crossing or dam, and "wetland type" is road or dam.

Prediction 2a: I compared upstream snag densities and total site (i.e. upstream + downstream) snag densities (snags per 100 m^2) between pairs of types. Per treatment densities were calculated using a total count per treatment at each site, i.e. pooling across transects. I also tested the prediction that within sites, the proportion of upstream snags was different at road crossings and beaver dams, using the ratio upstream snags: total snags. A Wilcoxon signed-ranks test, paired by site, was used for each of these analyses.

Prediction 2b: Vegetation zone width was calculated as the mean number of plots in each vegetation type (per transect). I used log-transformed average upstream meadow width, total site meadow width (pooled across treatments), and total site nonforest width (meadow + shrub) and a Wilcoxon signed-ranks test.

Prediction 2c: To test predictions about relative up- and downstream vegetation zone widths at road crossings compared to beaver dams I used a 2-factor split-plot ANOVA on rank transformed average zone width. Split-plot designs are a variation of a randomised complete block design intended for situations where there are no replicates of each combination of the factors, and where there is expected to be a significant effect from block variability (Underwood 1997, Quinn & Keough 2002). For these analyses, the factors tested were wetland type (beaver or road; fixed factor) and treatment (up- or downstream; fixed factor), blocking by site (random factor). Rank transformation is a technique in which the usual parametric statistical procedure is applied to the ranks of the data instead of to the data themselves (Conover & Iman 1981), and was used to deal with non-normality and outliers in the zone width data (Quinn & Keough 2002). A GLM procedure was used to permit designating appropriate error terms and interactions.

The model for the split-plot design was:

$Y_{ijk} = \mu + \tau_i + \rho_k + W_{ik} + \beta_j + (\tau\beta)_{ij} + E_{ijk}$

where Y_{ijk} = e.g. zone width

μ = overall mean

τ_i = main plot treatment effect (Factor A, Type) associated with i^{th} Type, where i = 1, 2 (i.e. beaver dam or road crossing)

ρ_k = block effect associated with k^{th} block, where k = Site (4,5,7,9,12,13)

β_j = subplot treatment effect (Factor B, Treatment) associated with Treatment, where j = 1,2 (i.e. upstream, downstream)

W_{ik} = main plot error (which is the interaction between Site and Type)

$(\tau\beta)_{ij}$ = interaction effect associated with i^{th} Type and j^{th} Treatment

E_{ijk} = residual error associated with subplots within main plots

Details of F-ratios are in Table A4.1.

Prediction 3a: I used stump densities for *Populus* (aspen and poplar) per type (beaver / road) at each site to measure beaver foraging intensity at dams and road crossings. Per treatment densities were calculated using a total count per treatment at each site, i.e. pooling across transects. The data were log transformed to correct for heteroscedasticity and compared using a Wilcoxon signed-ranks test.

Prediction 3b: I estimated the approximate basal area of the pre-beaver, unbrowsed stand as $ba_{stumps} + ba_{trees}$. I then compared the proportion of total *Populus* basal area that was stumps ($ba_{stumps} / (ba_{stumps} + ba_{trees})$). I also examined the relative abundance of stumps in different vegetation zones by a contingency table analysis of stump basal area (m^2 / $100m^2$) per zone (calculated using total stump basal area in each zone at each site, i.e. pooling across transects). A contingency table was used rather than a paired Wilcoxon test because some of the roads sites with stumps are not paired with associated beaver dams (sites 14,15,16).

2.3 Statistical Notes

All analyses were conducted using Systat 10.2.01 statistical software (Systat Software Inc. 2002). ANOVA's were done using the generalised linear model (glm) procedure in Systat because the general ANOVA procedure does not allow the user to specify fixed or random effects, error terms, and interactions, nor to define categorical variables.

3 RESULTS

3.1 Effects of Road Crossings

A summary of results for road crossing analyses is presented in Table 4.2.

Table 4.2 Summary of treatment effects at road crossings (treatment is upstream/ downstream)

Analysis	Result
snag density all species	not significant (p=0.398)
Populus snag density	not significant (p=0.484)
meadow zone width	significantly higher upstream (p=0.018)
shrub zone width	not significant (p=0.553)
nonforest zone width	not significant (p=0.235)
tree basal area all species	not significant (p=0.905)
Populus tree basal area	not significant (p=0.499)
spruce tree basal area	not significant (p=0.893)
Populus sapling density	not significant (p=0.767)
deciduous sapling density	not significant (p=0.678)
conifer sapling density	not significant (p=0.075)
proportion deciduous saplings	significantly higher upstream (p=0.046)

3.1.1 Snag Density

Prediction 1a: Snag density at road crossings did not differ between treatments at the sites studied (p=0.398) (Table A4.2). I was unable to study relative up- and downstream snag abundances of individual species since for all species except *Populus*, there were either too few snags, or snags were present at only a few sites. *Populus* snags were present at 8 of 9 sites. Although six of these sites had higher snag density downstream, treatment effect was not significant (p=0.484).

3.1.2 Riparian Vegetation Zone Widths

Prediction 1b: Average per treatment zone widths (meadow, shrub, and forest) were highly variable among sites (Table 4.3). Meadow zones were significantly wider upstream than downstream (p=0.018); in fact, at eight of the nine sites studied, the meadow zone was wider upstream (the ninth site had no meadow zone). Shrub zone width was not significantly different between treatments (p=0.553) nor was the total width of the non-forest vegetation zone (meadow + shrub) (p=0.235).

Table 4.3 Average vegetation zone width (m) per treatment at road crossing sites

Site	meadow		shrub		forest		non-forest	
	up	down	up	down	up	down	up	down
4	7	7	4	18	37	23	11	25
5	13.5	3	3	5	31.5	40	16.5	8
7	11	7	5	11	32	30	16	18
9	4	0	13	12	31	36	17	12
12	9	7	22	17	17	24	31	24
13	3	2	3	10	42	36	6	12
14	0	0	14	0	34	48	14	0
15	15	5	8	11	25	23	23	16
16	18	10.5	2	0	30	22.5	20	10.5
Average	8.9	4.6	8.2	9.3	31.0	31.4	17.2	13.9

Width represents distance from downslope edge to upland edge of each vegetation zone, averaged across transects within each treatment. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

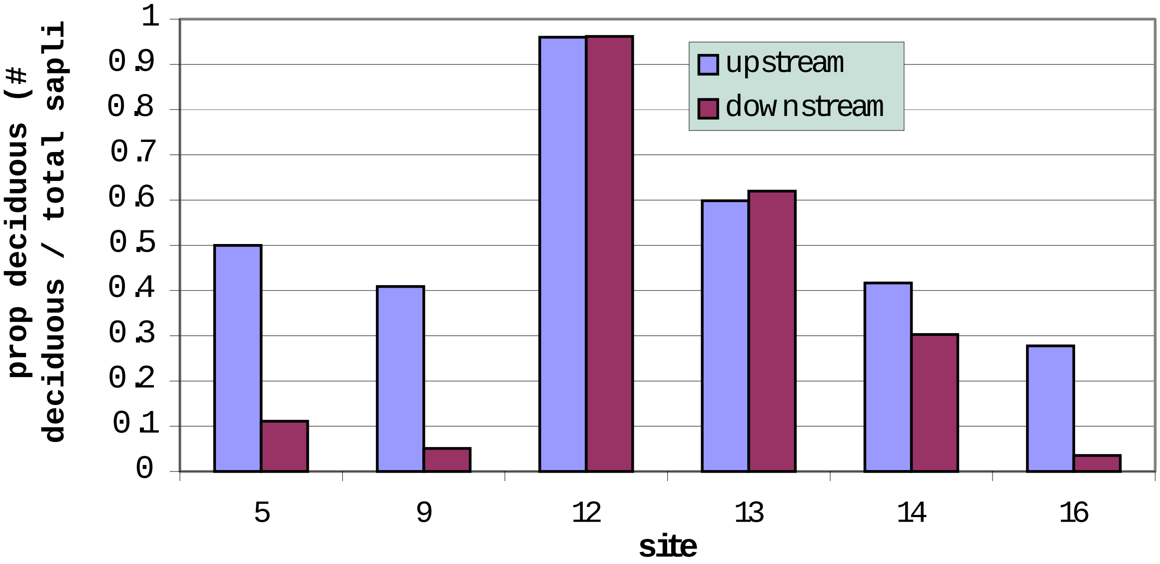
3.1.3 Forest Structure & Composition

Prediction 1c: Average tree basal area for all species combined did not differ between treatments (p=0.905, Table A4.3). Stem size class structure did not appear to differ between the treatments (Figure A4.1) although this was not tested statistically.

Populus and spruce were present in sufficient quantities at enough sites for species-level analyses. Mean size did not differ with treatment for these species (*Populus* p=0.499; spruce, p=0.893) nor did the size class distribution (Figure A4.2, A4.3).

Prediction 1d: Sapling densities varied widely with treatment among sites (Table A4.4). No significant per treatment differences in density were detected for *Populus* (p=0.767), nor for deciduous tree species combined (p=0.678). Only six of the nine road sites had mature conifer canopy as a seed source. Although four out of these six sites had more conifer saplings downstream than upstream, this difference was not significant (p=0.075). The proportion of deciduous saplings was higher upstream at five of these six sites (Figure 4.1, p=0.046).

Figure 4.1 Proportion of deciduous saplings per treatment at road crossings (only sites with conifer canopy as seed source)



Proportion deciduous saplings was calculated as (number deciduous / total saplings), pooling all transects within each treatment.

3.2 Comparison of Road Crossing and Beaver Dam Effects

Table 4.4 Summary of analyses comparing beaver dams and road crossings

Analysis	Variable	Contrast	Result
snag density	all species, upstream	between types*	not significant (p=0.581)
snag density	all species, type total per site^	between types	not significant (p=0.5)
proportion snags upstream	all species	between types	not significant (p=0.5)
meadow zone width	upstream	between types	not significant (p=0.917)
meadow zone width	average per type	between types	not significant (p=0.116)
meadow zone width	per treatment~	between treatments, within types	higher upstream at roads, higher downstream at beaver dams
		treatment x type interaction	*significant (p=0.008)*
nonforest zone width	average per type	between types	not significant (p=0.6)
nonforest zone width	per treatment	among sites	not significant (p=0.205)
		between types	not significant (p=0.436)
		between treatments, within types	not significant (p=0.409)
		treatment x type interaction	not significant (p=0.916)
sapling density	all deciduous	between types	not significant
proportion deciduous saplings	whole type	between types	not significant (p=0.173)
proportion deciduous saplings	*per treatment*	*among sites*	*significant (p=0.002)*
		between types	*significant (p=0.049)*
		between treatments, within types	not significant (p=0.787)
		treatment x type interaction	not significant (p=0.127)
stump density	*whole type*	*between types*	*significantly higher at dams (p=0.046)*
proportion of Populus felled	*whole type*	*between types*	*significantly higher at dams (p=0.028)*

*Type is wetland type, beaver dam or road crossing, within each paired site.
^Site consists of a paired road crossing and beaver dam along the same stream.
~Treatment is upstream or downstream at each beaver dam or road crossing.

3.2.1 Beaver Interaction with Road Crossings

Of the nine road crossing sites surveyed in this study, all had signs of beaver activity such as stumps and/or old dams within 20 m upstream. At five of these sites, there was clear evidence that beavers had plugged the culvert recently.

3.2.2 Snag Density

Prediction 2a: Only Site 5 did not have any snags at either the beaver dam or the road crossing. At the other sites, snag density showed no obvious patterns of being higher up- or downstream at either beaver dams or road crossings (Table A4.5). Although the average upstream snag density was slightly higher at beaver dams, this difference was not significant when site variability was taken into account (p=0.581). The total snag density (combining treatments) was higher at beaver dams at four of the five sites with snags but this difference was not significant (p=0.5). The proportion of snags upstream was also not significantly different between types (p=0.5).

3.2.3 Riparian Vegetation Zone Widths

Prediction 2b: Average vegetation zone widths appeared to be different between beaver dams and roads (Table 4.4) but these differences were highly variable among sites. Road crossings did not have significantly wider upstream meadow zones than beaver dams (p=0.917). Four of six sites had wider total (i.e. combining up- and downstream treatments) meadow zone at the beaver dam (Figure 4.2) but this difference was not statistically significant (p=0.116) nor was the width of the non-forest zone (p=0.600).

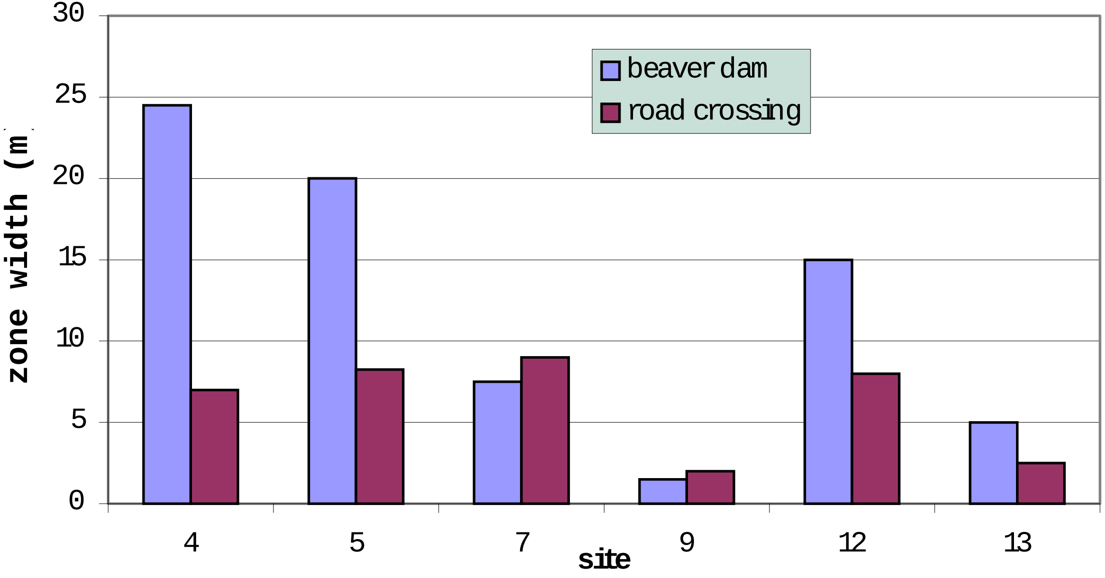
Table 4.5 Average vegetation zone widths* per treatment & type at each site

Site	BEAVER DAM						ROAD CROSSING					
	meadow		shrub		forest		meadow		shrub		forest	
	up	down	up	down	up	down	up	down	up	down	up	down
4	30	19.0	14	21	4	8	7	7	4	18	37	23
5	14	26	9	8	25	14	14	3	3	5	32	40
7	5	10	24	10	19	28	11	7	5	11	32	30
9	0	3	2	1	46	44	4	0	13	12	31	36
12	13	17	10	16	25	15	9	7	22	17	17	24
13	4	6	2	2	42	40	3	2	3	10	42	36
average	11	13.5	10.2	9.7	26.8	24.8	7.9	4.3	8.3	12.2	31.8	31.5

* data converted to m for ease of interpretation
Treatment is upstream or downstream of dam or road crossing.
Type is beaver dam or road crossing within each site.

Width represents distance from downslope edge to upland edge of each vegetation zone, averaged across transects within each treatment. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

Figure 4.2 Average meadow zone width (m) at beaver dams and road crossings. Data for individual sites are shown to highlight variability.



Width represents distance from downslope edge to upland edge of each vegetation zone, averaged across transects and treatments within each site. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

Prediction 2c: At road sites, the meadow zone appeared to be relatively wider upstream than downstream, compared to beaver dams where the downstream meadow zone was wider on average (Figure A4.4). A split-plot ANOVA analysis of this relationship showed a significant interaction between treatment (up- or downstream) and wetland type (beaver or road) (p=0.008, Table 4.5; note that a significant interaction term precludes statistical analysis of individual factor effects; Quinn & Keough 2001). Non-forest zone (meadow + shrub) appeared to be wider at beaver dams and wider downstream overall. There was no significant overall effect of treatment (p=0.409, Table 4.6) or wetland type (p=0.436) on non-forest zone width.

Table 4.6 Split-plot ANOVA table for effects of site, wetland type, and treatment on meadow zone width

Source	df	SS	MS	Fobs	p
site	5	703.25	140.65	4.979	*0.051*
wetland type*	1	121.5	121.5	4.301	(0.093)^
treatment~	1	6	6	0.733	(0.412)
treatment x type	1	88.167	88.167	10.774	*0.008*
site error	5	141.25	28.25		
error	10	81.833	8.183		

* beaver dam or road crossing
~ upstream or downstream

^ note that the significant interaction term precludes analysis of individual main effects (Underwood 1997)

Width represents distance from downslope edge to upland edge of each vegetation zone, averaged across transects and treatments within each site. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

Table 4.7 Split-plot ANOVA table for effects of site, wetland type, and treatment on nonforest zone width

Source	df	SS	MS	Fobs	p
site	5	653.125	130.625	2.192	0.205
wetland type*	1	42.667	42.667	0.716	0.436
treatment~	1	10.667	10.667	0.741	0.409
treatment x type	1	0.167	0.167	0.012	0.916
site error	5	297.958	59.592		
error	10	143.917	14.392		

* beaver dam or road crossing
~ upstream or downstream

Width represents distance from downslope edge to upland edge of each vegetation zone, averaged across transects and treatments within each site. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

3.2.5 Stumps and Foraging

Populus stumps were present at only three of the six road crossing sites; *Salix* stumps were present at five of the six road sites. The road crossing at site 13 did not have any stumps.

Prediction 3a: Stump density for *Populus* was higher at beaver dams than at road crossings at almost all sites (Table 4.8), and overall was statistically significant (p=0.046). There were too few road-crossing sites with stumps to compare stump density or proportion of total basal area per treatment, although no pattern of more stumps upstream or downstream seems apparent at either dams or roads when site differences are considered.

Prediction 3b: A much higher poportion of *Populus* trees had been felled at dams compared to roads (p=0.028, Table 4.9) although *Populus* trees were readily available at road crossing sites (Figure 4.3).

Table 4.8 Density of *Populus* stumps (number / 100m^2) per treatment, per wetland type, at each site

Site	BEAVER DAM			ROAD CROSSING		
	up	down	total	up	down	total
4	0.93	12.73	6.83	2.78	5.79	4.28
5	1.39	0.23	0.81	0.00	0.00	0.00
7	5.09	4.63	4.86	2.31	0.00	1.16
9	0.93	1.85	1.39	0.00	0.00	0.00
12	1.16	1.85	1.50	1.16	2.55	1.85
13	0.46	0.46	0.46	0.00	0.00	0.00
Average	1.66	3.63	2.64	1.04	1.39	1.22

Treatment is upstream or downstream of beaver dam or road crossing. Data are pooled across transects. *Populus* category includes stumps of both *P. tremuloides* and *P. balsamifera*, which could not always be distinguished.

Table 4.9 Proportion of total available *Populus* cut in each treatment for each site, calculated using basal area of stumps and trees

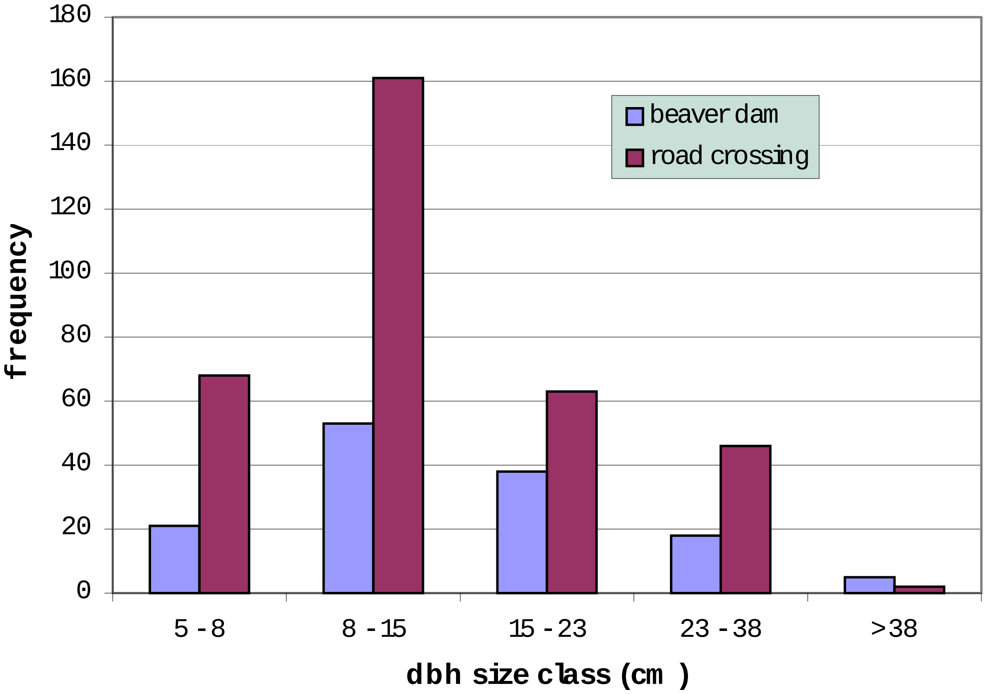
Site	BEAVER DAM			ROAD CROSSING		
	up	down	total	up	down	total
4	1.00	0.58	0.70	0.07	0.32	0.22
5	1.00	1.00	1.00	0.00	0.00	0.00
7	0.49	0.57	0.53	0.31	0.00	0.16
9	0.54	0.44	0.47	0.00	0.00	0.00
12	0.32	0.27	0.30	0.01	0.24	0.16
13	0.17	0.26	0.20	0.00	0.00	0.00
Average	0.59	0.52	0.53	0.07	0.09	0.09

Total basal area was calculated as $ba_{stumps} + ba_{trees}$ to recreate approximate pre-beaver stand; proportion cut was then calculated as (ba_{stumps} / ba_{total}).

Treatment is upstream or downstream of beaver dam or road crossing.

Data are pooled across transects.

Figure 4.3 Size class structure of *Populus* trees at road crossings and beaver dams, pooled across treatments and sites



Site consists of a paired road crossing and beaver dam along the same stream.
Type is wetland type, beaver dam or road crossing, within each paired site.
Treatment is upstream or downstream at each beaver dam or road crossing.
'Populus' includes both P. tremuloides and P. balsamifera.

4 DISCUSSION

4.1 Riparian Vegetation Changes at Road Crossings

My central research question was whether road crossings at defined stream channels in northeastern Alberta have a damming effect similar to beaver dams. I hypothesised that roads cause hydrological interruptions, raising upstream water tables and lowering them downstream. Predicted effects of such changes to water levels were greater numbers of snags upstream, greater tree size downstream, and wider non-forest riparian zones upstream.

The strongest evidence for intercepted flow at road crossings is the significantly wider upstream meadow zone. Two severe drought years preceded field sampling in Summer 2002, and water levels throughout the region were very low. The ærial photo analysis (Chapter 3) indicated that these meadow zones are a result of both foraging and pond-draining. The wide meadow zones at the study sites therefore represent a flooded area that had drained after severely lowered water levels during the drought.

There was no difference in snag density on either side of road crossings, nor did tree sizes differ. This result seems to indicate that road crossings are not raising upstream water levels. Tree death due to flooding is strongly related to both the depth and duration of inundation (Green 1947, Hosner & Boyce 1962), and response to draining depends on climatic relations and site-specific factors such as properties of the soil and water, and topography, rainfall, etc. (Stoeckeler 1963). Moreover, road structures age and mature with time, and their effects can take decades to fully manifest (e.g. Reid et al. 1997, Gucinski et al. 2001). In his study of road damming effects, Jeglum (1975) observed that water ponding and tree death were gradual processes, with the full effects not becoming apparent for almost 20 years. The road crossings studied here ranged from 9 to 43 years (see Chapter 3). Even though there is no way of knowing the appropriate time-frame at which to study road effects in this region, some of the among-site variability may be explained by the large range in road age.

Although not statistically significant, the observed overall greater number of *Populus* snags downstream of road crossings is consistent with changes in soil moisture levels but the pattern is the opposite of what I had hypothesised. One possible explanation is that there was a pronounced downstream lowering of water table that had more of an effect than an upstream rise, and that downstream *Populus* were killed by drought stress. Studies of riparian disturbance due to anthropogenic dams have shown increased *Populus* death downstream as water levels are lowered (Rood & Heinze-Milne 1988, Rood & Mahoney 1990). These studies were for *Populus deltoides*, while my study sites had *P. tremuloides* and *P. balsamifera*. These two species exhibit different responses to raised water tables: while *P. balsamifera* is tolerant of saturated soils, *P. tremuloides* is not (Perala 1990; Zasada & Phipps 1990). I was not able to distinguish the two species in the snags studied, which may have contributed to the high variability of my data, and obscured any effects of changed water tables.

Similarly, pooling saplings of different species may have obscured my ability to detect statistical differences between treatments, and did impede interpretation of significant results. I had predicted a higher proportion of deciduous saplings upstream of road crossings due to raised water table. In the field I had difficulty distinguishing black spruce and white spruce saplings, and so for my analyses I pooled saplings into 'deciduous' and 'coniferous' categories. *Populus balsamifera* seedlings exhibit better survivorship than *P. tremuloides* in saturated soil conditions (Landhäusser et al. 2003) and black spruce is much more moisture tolerant than white spruce. I was unable to distinguish the two spruce species at the sapling stage. This study found a significantly greater proportion of deciduous saplings upstream at road crossings but the split-plot ANOVA analyses comparing beaver dams and road crossings did not detect an overall treatment effect. This contradiction may be due to site differences (there were significant site and type effects) but may also reflect the different species composition among sites and species specific response.

The small sample size, high among-site variability, and differences in road age, topography, and other edaphic factors among sites restrict my ability to draw clear and simple conclusions about riparian disturbance due to hydrological interruptions caused by road crossings. The interaction between beavers and road crossings means that my analysis is actually of the road-plus-beaver unit. Pervasive beaver activity makes it impossible to separate whether impoundment effects at my sites were due to the road crossing itself or to sporadic beaver plugging of the culverts. I could not find, and therefore did not study, any road crossings unaffected by beaver activity. My results therefore cannot be extended to conclusions about hydrological effects of road crossings themselves. In addition, roads are not isolated features of the landscape: their effects are sometimes closely linked to basin-wide changes due to whatever industrial activities have necessitated road construction (Gucinski et al. 2001). AlPac's FMA is criss-crossed by a lattice of potentially confounding effects, ranging from road rights-of-way and buried pipelines adjacent to roads, to the sheer abundance of disturbances such as cutblocks, well-sites, and seismic lines in adjacent upland areas, not to mention the density of the road network itself.

4.2 Beaver Use of Road Crossing Structures

In the boreal mixedwood forest of northern Alberta, beavers and road crossings appear to be inextricably linked. Only the largest culverts and bridges escape being plugged on a regular basis. In a survey of resource managers and wildlife control officers, D'Eon et al. (1995) found that this interaction is a problem throughout North America.

Many government publications and internal natural resource department documents deal with "beaver problems" with respect to culvert / bridge blocking. Almost without exception, these reports focus on management – that is, how to effectively remove or thwart the beavers – rather than on understanding the factors affecting the problematic beaver activity. In general, features that influence beaver dam location include geomorphology (Johnson & Naiman 1990b, McComb et al. 1990), vegetation (Barnes & Mallik 1997), and upstream watershed area (Howard & Larson 1985, Barnes & Mallik 1997). Roadbed construction constitutes a local anthropogenic alteration to geomorphology that is very attractive to beavers as they seek out logical "pinch points" in waterways that maximize flooding potential with minimal construction effort. There are very few studies in the primary literature of beaver interactions with anthropogenic structures. McComb et al. (1990) found that dam placement was not affected by distance to bridges, roads, or buildings if habitat requirements were met but they did not specifically examine interactions between beavers and road-crossing structures. Jensen et al. (1999, 2001) examined this issue from the other perspective: comparing dammed and undammed culverts throughout the state of New York. They found that culvert area was the strongest predictor of whether beavers would dam the road crossing. Habitat-related factors such as the amount of roadside clearing area, shrub cover, and distance to the nearest clump of food trees did not differ between blocked and unblocked culverts. In flat areas of the state, the total amount of woody vegetation adjacent to the road was also a predictive component of the model but still had less explanatory power than culvert size (Jensen et al. 1999).

These results led them to speculate that beavers plug culverts because they are "hard-wired for sound": that is, the sound of water flowing through a constriction (a restrictive culvert) induces dam-building activity regardless of habitat availability near the road.

In my study, road crossings experienced significantly less foraging than their associated beaver dams, despite similar forest composition in each pair and clear evidence of a dam at all road crossings. Thus, although beavers block culverts and create ponds at road crossings, they do not use the surrounding habitat in the same way that they utilise habitat at their own dams. Active removal of beavers and dams from road crossings probably prevents beavers from fully utilising the surrounding habitat, although without further study it is a matter of conjecture whether this difference fully accounts for lower foraging intensity at roads.

4.3 Riparian Vegetation Changes at Road Crossings and Beaver Dams

A central hypothesis of this study was that road crossings create more permanent hydrological interruptions than beaver dams. If this were the case, riparian changes (such as tree death upstream) should be more apparent at road crossings. I found no significant differences between road crossings and beaver dams in snag density, riparian zone width, or sapling density – the factors I identified as indicators of water-level change. The interaction of beavers with culverts, however, makes this comparison one between beaver dams and the road-plus-beaver unit: so perhaps it is not surprising that there are no significant differences between the two. In fact, the cycle of beaver and dam removal at culverts, re-colonisation, and re-removal may make impoundments at road crossings even more transitory than beaver ponds.

4.4 Conclusions – are roads a permanent beaver dam?

Road crossings did not demonstrate different tree survival or growth upstream and downstream, as measured by snag densities and tree basal areas. Road crossings did have wider meadow zones upstream; meadow zones were interpreted as representing a combined area of previously area of raised water table and impoundment that had drained in the 2000-02 drought. These results suggest an increase in water levels and soil moisture upstream of road crossings that have been influenced by beavers. On the whole, beaver dams and road crossings had similar effects on riparian vegetation, and beaver-like effects were not more pronounced at road crossings. Vegetation zone widths were much more variable at beaver dams than at roads. However, the extensive interaction between beavers and culverts confounded these results, and converted the potential impacts of road crossings to a road-plus-beaver effect. Despite their apparent obsession with blocking culverts, beaver foraging activity was significantly lower at road crossings than at beaver dams, implying that from a beaver's perspective, a road crossing is *not* simply a human beaver dam.

Chapter 5 Beaver Effects on Riparian Stand Dynamics

1 INTRODUCTION

In eastern North America, beavers (*Castor canadensis*) are considered a keystone species affecting wetland diversity and abundance and structuring riparian communities (e.g. Naiman et al. 1986). Flooding and tree-felling, the two most obvious impacts that beavers have, both can extensively alter riparian communities. By creating ponds, beaver activity can have a significant influence on the regional distribution and abundance of wetland vegetation types (Hammerson 1994, Syphard & Garcia 2001). Through size- and species-selective foraging of trees and shrubs, beaver foraging directly alters riparian forest structure (e.g. Barnes & Dibble 1988, Johnston et al. 1990a, Donkor & Fryxell 1999) and relative species abundances (Wright et al. 2002). Selective beaver foraging also can affect successional pathways by changing nutrient cycling (Pastor & Naiman 1992) and releasing understory conifers from competition (Naiman et al. 1988b, Johnston & Naiman 1990a, Donkor & Fryxell 1999). Beaver activity, therefore, structures riparian and wetland communities and affects habitat availability for a large variety of other species.

Rowe (1961) stated that lack of knowledge about biological dynamics in the boreal forest is a major constraint to its management – a sentiment echoed by Schneider et al. (2003) in their recent examination of industrial impacts in northern Alberta. Although an extensive literature exists on beavers in eastern boreal forests, they have rarely been studied in western mixedwood ecosystems. The boreal mixedwood forest is quite different in both topography and vegetation composition from eastern boreal forests (Johnson et al. 1995, Pojar 1996) and thus the impacts and role of beavers may differ as well.

This study sought to improve our understanding of beaver foraging and its impacts in the boreal mixedwood. Specific objectives of this study were:

1) *To measure how beaver foraging and dam-building affect the structure and composition of riparian vegetation in boreal mixedwood forests.*

This project was initially designed to compare beaver dams and road crossings; the analyses in this chapter therefore are constrained by the lack of non-beaver "control" sites against which to compare beaver activities. Nonetheless, the detailed field measurements provide an opportunity for in-depth natural history analysis and permit comparisons between the upstream and downstream impacts of beaver activities.

Studies of anthropogenic dams have shown changes in tree growth rates up- and downstream of the dam (e.g. Rood & Mahoney 1990, O'Connor 2001). At beaver dams in other areas of North America, changes to surface and subsurface flow were reported to cause effects such as tree death upstream due to flooding, and increased tree growth downstream due to lowered water tables (Wilde et al. 1950). Based on these observations, I predicted that there would be increased numbers of snags upstream of beaver dams, and that downstream trees would be larger than upstream trees. Raised water tables upstream could also result in wider non-forest riparian zones (i.e., sedge, grass, and shrub zones), due to the greater tolerance these plants have for saturated soils. Such predicted changes to water tables might alter relative sapling densities since saplings of different species experience differential survival following changes to soil moisture (Green 1947, Hosner 1960). In general, *Populus* spp. and black spruce (*Picea mariana*) can tolerate flooded roots where white spruce (*P. glauca*) cannot.

Beavers are considered central-place foragers (Schoener 1979), with their ponds as a central location to which they return between foraging expeditions, or to which they bring back food and construction materials. Their foraging efforts are thus concentrated close to their ponds. Beavers are also increasingly size- and species-selective with increasing distance from water's edge (e.g. Jenkins 1975, 1980). By analysing beaver use-availability of different species and size classes, and whether these change with distance from water's edge, I hoped to provide valuable data on beaver habitat use in boreal mixedwood forests.

2) *To examine the potential effects of beaver activities on riparian succession and dynamics in boreal mixedwoods.*

The species-selectivity of beaver foraging can lead to changes in riparian forest composition. With deciduous tree removal, the relative importance of deciduous and coniferous trees can change (Donkor & Fryxell 1999) and can lead to increased conifer growth (Lawrence 1952, Barnes & Mallik 2001). Notionally, the path of succession in boreal mixedwood forests is from aspen stands with a white spruce understory, through mixed stands, to mature white spruce stands (Johnson et al. 1995, but see critique in Rowe 1961). In the boreal mixedwood, therefore, beavers may be converting mid-seral mixed stands to late-successional coniferous forests not only directly, through felling, but also through competitive release of understory conifers (Lawrence 1952, Naiman et al. 1988b, Johnston & Naiman 1990a). By estimating pre-browse forest composition (using the evidence left behind by beaver stumps), and comparing pre- and post-browse vegetation, I aimed to test the hypothesis that beavers convert mixed- or deciduous stands to conifer stands. I predicted that beaver foraging would decrease the relative dominance of deciduous trees and increase that of conifers. I also predicted that the combination of selective foraging and changes to water levels would alter the relative proportions of deciduous and conifer saplings upstream and downstream of the dams. Further, I predicted that the relative abundance of deciduous saplings would increase with distance from water's edge. Changes to relative sapling abundance may influence successional pathways and future forest structure in riparian areas around beaver ponds.

2 STUDY AREA AND METHODS

I conducted this study on six active beaver dam sites in AlPac's forest management area (FMA) in northeastern Alberta (Figure 1.2). A description of the study area, study site selection, and field techniques is provided in Chapter 1.

Due to the study's small sample size and non-normal data distributions, non-parametric tests were used for all analyses (refer to Chapter 4 for a discussion of this choice). In all analyses here, "site" refers to each beaver dam and "treatment" is upstream or downstream location at the beaver dam.

Each plot along the transects was designated as representing meadow, shrub, or forest vegetation community (see Chapter 1 for details). These different riparian community zones were hypothesised to have been structured by beaver activity – raised water tables and tree-felling create a sedge and grass meadow zone immediately adjacent to water's edge. Continued beaver presence would maintain this meadow but over time without beaver activity, the meadow would develop into shrub and then a forest community.

2.1 Site Age

An air photo time sequence analysis was used to determine approximate ages for the dams used in this study (see Chapter 3).

2.2 Mean Tree Size

I used a mixed-model 2-factor ANOVA to test the hypothesis of larger tree sizes downstream of beaver dams. A mixed-model ANOVA has a mix of fixed and random factors being tested. I used log transformed basal area of trees measured at each site, pooled across transects within each treatment. The two factors were treatment (up- or downstream location) as a fixed factor, and site as a random factor; the model tested for effects of both factors as well as a treatment x site interaction. For these analyses I used data only for the most common tree species (*Populus* (aspen and poplar), *Picea* (white and black spruce), *Pinus* (jack and lodgepole pine), and *Abies* (balsam fir)).

2.3 Snag Density

I used a Wilcoxon signed-ranks test to compare differences in snag abundance with treatment (total number of snags per treatment, pooled across transects). I conducted this analysis for all species combined, for just conifer species, and at the species level for *Populus* (aspen and poplar). I also pooled snag abundances across sites and compared snag distributions in the different vegetation zones.

2.4 Riparian Vegetation Zone Widths

A Wilcoxon signed-ranks test was used to compare average vegetation zone widths within treatment at beaver dams. I calculated average zone widths as the mean number of plots in each vegetation zone, within each treatment at each site (averaged across transects). I used a contingency table analysis of overall average zone widths (i.e. average of all sites) to test the hypothesis of relatively wider non-forest zone widths upstream.

2.5 Beaver Foraging

I quantified past beaver foraging by counting and measuring the size and species of beaver-chewed stumps (of any age), > 1 cm diameter at stump height (approximately 30 cm). For these analyses I used the basal area of all *Populus* stumps (*P. tremuloides* and *P. balsamifera* combined due to inability to distinguish many stumps) measured at each site, pooled across transects. Data were log-transformed to stabilise among site variance.

I used a mixed-model 2-factor ANOVA to test for differences in stump sizes between treatments. I used individual stump basal areas in each treatment at each site. The two factors were treatment (up- or downstream) as a fixed factor, and site as a random factor; the model tested for effects of both factors as well as a treatment x site interaction.

To test if stump size decreases with distance from water's edge I applied a linear regression of stump basal area (individual measurements, pooled across treatments and sites) and distance from water's edge. I also performed separate regressions of each treatment.

In an attempt to find a better model, I then conducted 2-factor ANOVA's of the effects on stump size of site and distance (distance and site both random.

Most studies of the size-distance relationship of beaver foraging have used the high water mark to represent 0 distance from water's edge. I sampled during a drought where I presumed that the meadow zone in large part represented formerly flooded area (confirmed by analyses in Chapter 3). Therefore, I conducted one further analysis assuming that the upland edge of the meadow zone represented the former water's edge, and used the beginning of the shrub zone as 0 distance from water's edge. I conducted a linear regression to test the hypothesis that stump size declined with distance from this new "water's edge".

I examined beaver use / availability for *Populus* by looking at the % cut and uncut per size class. For this analysis, I pooled all stumps and trees across treatments. To analyse use / availability in the different vegetation zones, I pooled across sites. I did not conduct statistical analyses on this use / availability data.

2.6 Sapling Density

A Wilcoxon signed-ranks test was used to test for differences in per treatment sapling abundance and proportion of saplings that were deciduous (number deciduous / total number of saplings) at each site. The '*Populus*' category consisted of saplings of both trembling aspen and balsam poplar while 'deciduous' also included paper birch (*Betula papyrifera*); the 'conifer' category includes all saplings of spruce (*Picea*), pine (*Pinus*), and balsam fir (*Abies lasiocarpa*).

I tested for a relationship between sapling density and distance from water's edge by linear regression for both *Populus* and conifer saplings. For this analysis I used plot as a distance measure (96 plots per site), and average sapling density per plot as a dependent variable. Average sapling density was calculated by pooling per plot sapling counts across transects and sites. For this analysis, average conifer sapling abundances were log transformed to meet the assumption of heteroscedasticity (using the function log(average conifer sapling abundance + 0.08), where 0.08 is ½ of the smallest non-zero value).Since sapling abundance was highly variable among sites I also did mixed-model 2-factor ANOVA analyses with distance as a fixed factor, and site a random factor.

2.7 Importance Value

I approximated forest composition changes before and after recent beaver foraging, as determined by detected stumps, using an importance value calculation (as per Johnston & Naiman 1990a). Importance values are a measure of relative species dominance that balances density, basal area, and frequency of each category (species, size class, etc). Relative frequency is the number of plots with species x, as a ratio of the total number of plots sampled. Relative density is the total number of stems of species x, as a ratio the total number of stems of all species combined. Relative basal area is the total basal area of species x, as a ratio of the total basal area of all species combined. The importance value of species x is then calculated as the mean of relative frequency, relative density, and relative basal area.

Importance values were calculated as:

$$IV_x = \frac{RF_x + RD_x + RB_x}{3}$$

where IV = importance value of species x
x = species
RF_x = relative frequency of species x
RD_x = relative density of species x
RB_x = relative basal area of species x

and $$RF_x = \frac{\text{number of plots with species x}}{\text{total number of plots}} \times 100$$

$$RD_x = \frac{\text{number of stems of species x}}{\text{total number of stems}} \times 100$$

$$RB_x = \frac{\text{basal area of species x}}{\text{total basal area}} \times 100$$

I used stumps as evidence of the "pre-browse" stand and added sampled stumps and trees to reconstruct forest composition before beaver foraging. For example, pre-browse basal area = $ba_{trees} + ba_{stumps}$. This analysis may slightly over-estimate pre-browse conditions, since the remaining trees will have grown. As well, I did not estimate stump age. Considering the fairly large average stump size (see Table 5.6), and the relatively young age of most of the dam sites (<15 years, see Chapter 3), I think it is unlikely that any stumps represented trees that were not already standing when the beaver arrived.

At each site, I calculated pre-browse and post-browse importance values for *Populus* spp. and conifers. I calculated importance values both per treatment, and for the overall site. I combined all species in calculations of total number of stems and total basal area (i.e., including species represented by only a few individuals, such as paper birch). I then compared the difference in pre-browse and post-browse importance values for *Populus* and conifers at each site, using Wilcoxon signed-ranks tests. I also used a Wilcoxon signed-ranks procedure to test differences in per treatment importance values of conifers after beaver browsing.

2.8 Statistical Notes

All analyses were conducted using Systat 10.2.01 statistical software (Systat Software Inc. 2002). ANOVA's were done using the generalised linear model (glm) procedure in Systat because the general ANOVA procedure does not allow the user to specify fixed or random effects, error terms, and interactions, nor to define categorical variables. Regressions were also done using the glm procedure since the linear regression feature does not allow categorical variables.

3 RESULTS

A summary of all statistical analyses and results is presented in Table 5.1.

Table 5.1 Summary of statistical analyses at beaver dams

treatment is upstream or downstream of dam
* for variables where several analyses were conducted, the lowest p-value is reported here

variable	**species**	**contrast**	**result**
average tree basal area	all species combined	**among sites**	**significantly different (p=0.000)**
		between treatments	not significantly different (p=0.522)
		treatment x site interaction	**significant interaction (p=0.002)**
average tree basal area	*Populus*	**among sites**	**significantly different (p=0.000)**
		between treatments	not significantly different (p=0.096)
		treatment x site interaction	not significantly different (p=0.897)
average tree basal area	conifers combined	**among sites**	**significantly different (p=0.000)**
		between treatments	not significantly different (p=0.535)
		treatment x site interaction	**significant interaction (p=0.000)**
snag abundance	all species combined	between treatments	not significantly different (p=0.462)
snag abundance	*Populus*	between treatments	not significantly different (p=0.893)
snag abundance	conifers combined	between treatments	not significantly different (p=0.345)
meadow zone width	--	between treatments	not significantly different (p=0.249)
shrub zone width	--	between treatments	not significantly different (p=0.893)
relative zone widths	--	between treatments	not significantly different (alpha = 0.05)
stump size*	*Populus*	between treatments	not significantly different (p=0.879)
		among sites	not significantly different (p=0.089)
		treatment x site interaction	**significant interaction (p=0.001)**
		relationship with distance	significant (p=0.006)
		distance x site interaction	no significant interaction (0.802)

Table 5.1 (cont'd) Summary of statistical analyses at beaver dams

treatment is upstream or downstream of dam

* for variables where several analyses were conducted, the lowest p-value is reported here

variable	**species**	**contrast**	**result**
sapling density*	*Populus*	between treatments	not significantly different (p=0.463)
		relationship with distance	not significant (p=0.315)
		among sites	**significantly different (p=0.000)**
		distance x site interaction	**significant interaction (p=0.000)**
sapling density*	conifers combined	between treatments	not significantly different (p=0.207)
		relationship with distance	**significant increase with distance (p=0.033)**
		among sites	**significantly different (p=0.000)**
		distance x site interaction	**significant interaction (p=0.000)**
proportion deciduous saplings		between treatments	not significantly different (p=0.463)
importance value	*Populus*	**pre / post browse**	**significantly lower post-browse (p=0.028)**
		between treatments	not significantly different (p=0.225)
importance value	conifers combined	**pre / post browse**	**significantly higher post-browse (p=0.028)**
		between treatments	not significantly different (p=0.116)

3.1 Mean Tree Size

Total basal area in the forest zone was quite different between sites (Table A5.1). Average tree basal area of all species combined was higher upstream at 5 of the 6 study sites (Table 5.2).

Table 5.2 Average tree basal area (m2) per treatment for *Populus*, conifers, and all species combined, at each site

Site	*Populus*		conifer		all species	
	up	down	up	down	up	down
4	0.000	0.012	0.040	0.000	0.040	0.012
5	0.000	0.000	0.017	0.023	0.017	0.023
7	0.037	0.035	0.006	0.000	0.043	0.035
9	0.010	0.011	0.012	0.007	0.021	0.018
12	0.032	0.043	0.114	0.000	0.146	0.043
13	0.017	0.020	0.013	0.008	0.030	0.028
Average	0.0159	0.0201	0.0335	0.0063	0.0493	0.0264

treatment is upstream or downstream of beaver dam.

'Populus' category includes P. tremuloides and P. balsamifera

There was a significant effect of site on basal area of all species combined (p=0.000, Table 5.3). Treatment effect was not statistically significant (p=0.522). There was a significant effect of site x treatment interaction (p=0.002).

Table 5.3 ANOVA table for effects of treatment and site on tree basal area, for all species combined

Source	SS	df	MS	F-ratio	p-value
treatment*	0.676	1	0.676	0.474	0.522
site	106.181	5	21.236	57.36	*0.000*
site x treatment	7.125	5	1.425	3.849	*0.002*
error	234.352	633	0.37		

r2 = 0.360, n = 645

* upstream or downstream

Site had a significant effect on *Populus* tree size (p=0.000, Table 5.4). Average *Populus* basal area was lower upstream at all 4 sites that had trees both upstream and downstream but this effect was not significant (p=0.096). There was also no significant interaction between site and treatment.

Table 5.4 ANOVA table for effects of treatment and site on individual tree basal area, for *Populus* trees

Source	SS	df	MS	F-ratio	p-value
treatment*	0.503	1	0.503	5.748	0.096
site	20.123	4	5.031	11.448	*0.000*
site x treatment	0.262	3	0.087	0.199	0.897
error	52.294	119	0.439		

r2 = 0.340, n = 128

* upstream or downstream

'Populus' is P. tremuloides and P. balsamifera combined.

Data have been pooled across transects within each treatment at each site.

There was a significant effect of site (p=0.000) on conifer basal area (Table 5.5). Average conifer basal area was higher upstream than downstream at 5 of 6 sites, but the difference was not significant (p=0.535). The site x location interaction was significant (p=0.000). Single-species tests were not done because there were too few sites with species both up and downstream.

Table 5.5 ANOVA table for effects of treatment and site on individual tree basal area, for conifer trees

Source	SS	df	MS	F-ratio	p-value
treatment*	1.16	1	1.16	0.488	0.535
site	62.818	4	15.704	49.313	*0.000*
site x treatment	7.125	3	2.375	7.458	*0.000*
error	160.508	504	0.318		

r2 = 0.347, n = 513

* upstream or downstream

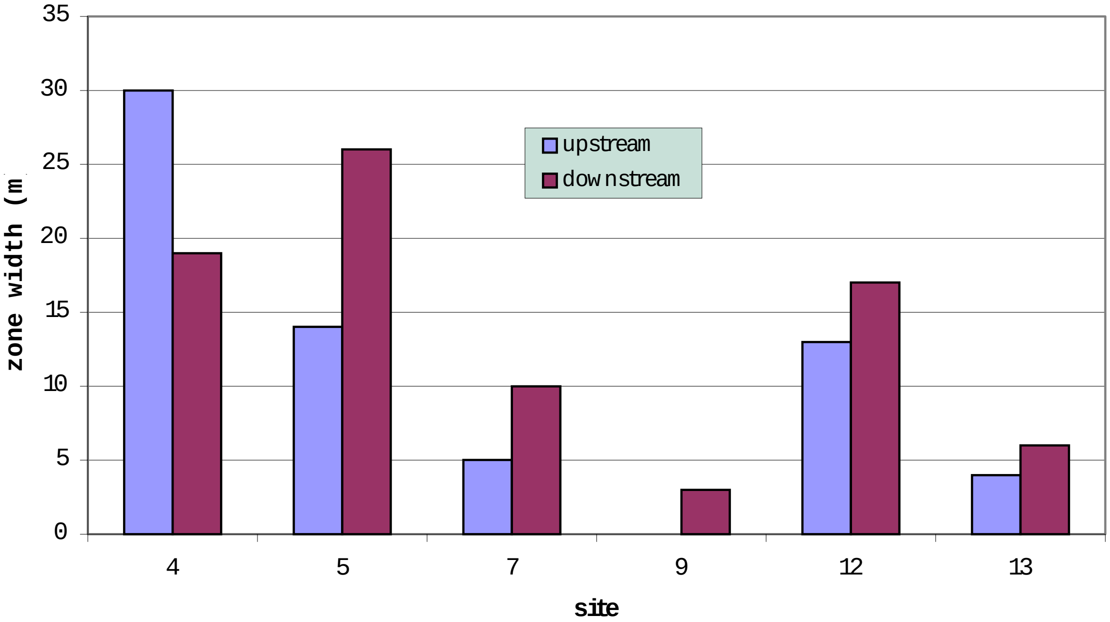
3.2 Snag Density

Four of the six sites had more total snags upstream than down (Table A5.2) but the difference was not significant ($p=0.462$). Snag abundance did not differ between treatments for either *Populus* ($p=0.893$) or conifer ($p=0.345$) snags. Pooling across all sites, the majority of snags were found in the forest zone (Figure A5.1).

3.3 Riparian Vegetation Zone Widths

Vegetation zone widths were highly variable between sites (Table A5.3, Figure A5.2). At 5 of the 6 sites, meadow zones were wider downstream (Figure 5.1) but the difference was not significant ($p=0.249$). Shrub zone width was not significantly different with treatment ($p=0.893$, Figure A5.3). There was no significant difference in relative average vegetation zone widths up- and downstream ($\chi^2 = 2.07$, df = 2, $\chi^2_{\text{crit}(0.05,\ 2)} = 5.991$; Table A5.4). Dam ages were estimated from time-series aerial photos (see methods in Chapter 3). The two new sites (<1 year old, sites 9 and 13) had the narrowest meadow and shrub zones while the two oldest sites (sites 4 and 5, 35 and 14 years respectively) had the widest meadow zones.

Figure 5.1 Average meadow zone width (m) per treatment at each site. Data for individual sites are shown to highlight variability.



Width represents distance from downslope edge to upland edge of each vegetation zone, averaged across transects within each treatment at each site. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

3.4 Beaver Foraging

At the six study sites, beavers used *Populus* trees almost exclusively (Table 5.6). Only one paper birch (*Betula papyrifera*) and no alder (*Alnus crispa*) stumps were found, however since few trees of these species were available this lack of stumps may simply reflect low availability. There were 2 white spruce (*Picea glauca*) stumps at Site 13 but no other conifer stumps were found at any sites, even though conifer trees overall were more abundant than *Populus* by 5:1. There were numerous *Salix sp.* stumps (288) but only 4 of them were >5 cm diameter stump height (DSH). The study design did not include counts of available *Salix* stems <5 cm dbh, so no analyses of use / availability were possible. Although other studies have documented beaver use of some of the other shrub species present (e.g *Alnus* spp., *Corylus cornuta*, *Betula* spp.), I did not find a single stump of any other shrub species at any of my six beaver dam sites[2].

Table 5.6 Number of trees and beaver stumps per species at beaver dams

species	stumps	trees
*Populus sp.**	144	135
paper birch	1	10
Alnus crispa	0	15
conifer~	2^	519
Total	147	679

* aspen (*P. tremuloides*) and poplar (*P. balsamifera*) combined
~ combined *Picea* (spruce), *Pinus* (pine), and *Abies* (fir) species
^ both were spruce stumps, at site 13

Mean stump size varied widely across sites (Table 5.7) but an ANOVA analysis of the effects of site and treatment did not show a significant site effect (p=0.822, Table 5.8). There was no significant difference in stump basal area between treatments (p=0.879), however, there was a significant treatment x site interaction (p=0.001).

Table 5.7 Average stump diameter for beaver-felled *Populus* stumps, per treatment, at each active beaver dam site. Stumps were measured at approximately 30 cm.

Site	**stump dsh (cm)**	
	upstream	downstream
4	25.88 (4)	5.38 (55)
5	9.2 (6)	15.2 (1)
7	15.3 (22)	19.15 (20)
9	14.55 (4)	15.44 (8)
12	18.52 (5)	16.45 (12)
13	16.4 (2)	16.4 (2)
Average	16.6	14.7

(number of stumps in brackets)

---

[2] One of the road sites analysed in Chapter 3 had numerous *Alnus rubra* stumps.

Treatment is upstream or downstream of dam.
"*Populus*" is *P. tremuloides* and *P. balsamifera* combined.

Table 5.8 ANOVA table of effects of treatment and site on stump basal area

Source	SS	df	MS	F-ratio	p-value
treatment*	0.314	1	0.314	0.026	0.879
site	5.686	5	1.137	0.438	0.822
site x treatment	61.497	5	12.299	4.733	*0.001*
error	327.402	126	2.598		

r2 = 0.376, n = 138
* upstream or downstream

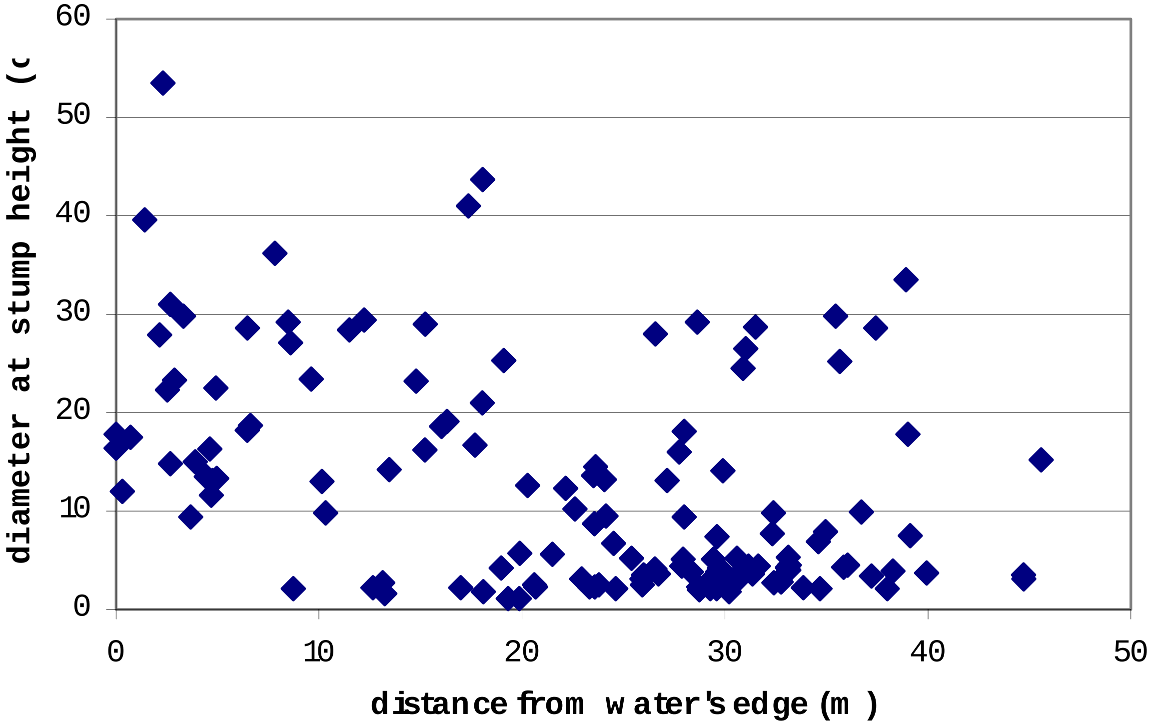
Data are for stumps of *P. tremuloides* and *P. balsamifera*.

Fifty percent of stump basal area measured in the 48 m transects was cut within 15 m of water's edge, and ninety percent within 33 m (refer to Chapter 3). Most plots with *Populus* stumps were in the shrub and forest zone while *Salix* stumps were found in the meadow zone (Figure A5.4). Pooled across treatments and sites, stump basal area tended to decrease with distance from water's edge (Figure 5.2) but the relationship was not clear. A regression was statistically significant but explained little of the variation (n=138, r^2=0.187, p=0.000).

The regression equation for stump basal area with distance was:

log(stump basal area) = 0.904 – 0.072 (distance)

Figure 5.2 Relationship between stump diameter (cm) and distance from water's edge (m) at active beaver dams



Data are pooled across treatments and sites. Stump diameter was measured at approximately 30 cm height for all stumps > 1 cm diameter at stump height. Distance from water's edge is distance perpendicular from water's edge heading towards upland. Data are for stumps of *P. tremuloides* and *P. balsamifera*.

A decrease in stump basal area with distance from water's edge was slightly more apparent upstream of the dam than downstream (Figure 5.3). Linear regressions of each treatment separately were both significant, but model fit did not improve. For the upstream treatment, the regression model was:

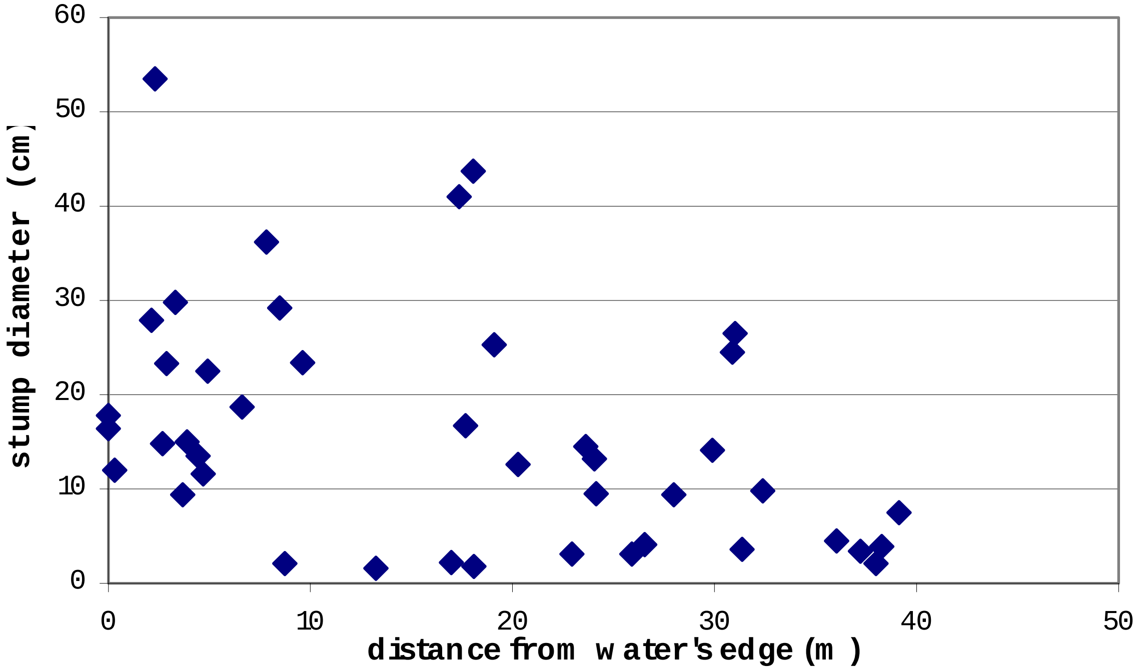
log(stump basal area) = 1.079 – 0.068 (distance) (n=43, r^2=0.196, p=0.003).

For the downstream treatment, the regression model was:

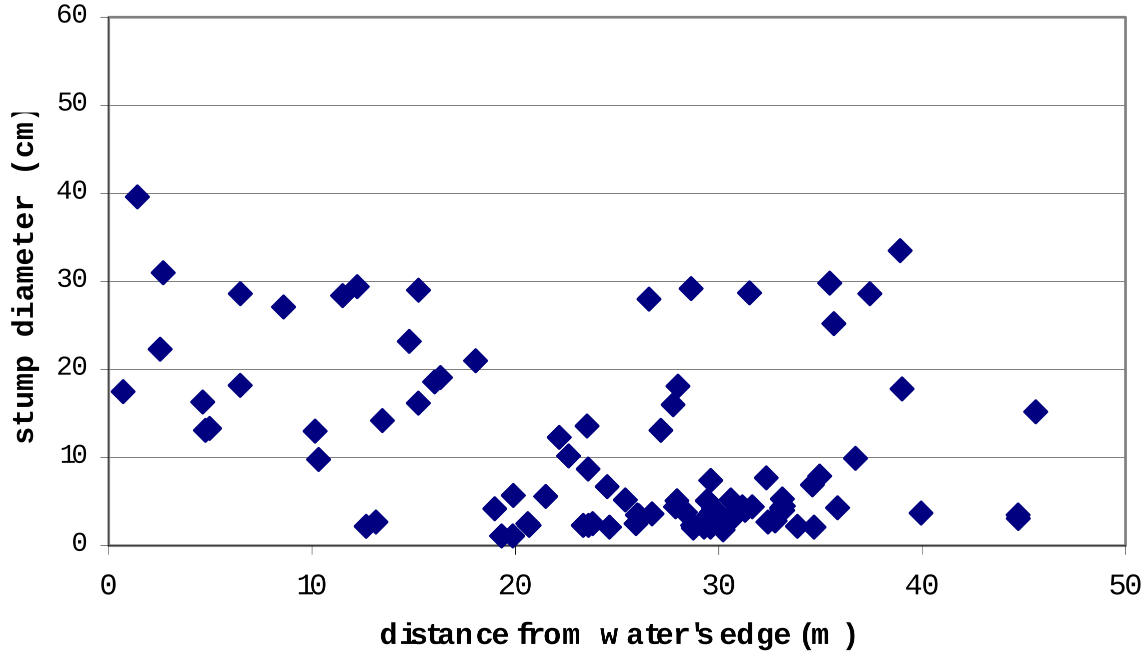
log(stump basal area) = 0.656 – 0.067 (distance) (n=95, r^2=0.135, p=0.000).

Figure 5.3 Relationship between stump diameter (cm) and distance from water's edge (m) per treatment at active beaver dams, pooled across sites

a) upstream



b) downstream



Treatment is upstream or downstream of dam. Stump diameter was measured at approximately 30 cm height for all stumps > 1 cm diameter at stump height. Distance from water's edge is distance perpendicular from water's edge heading towards upland. Data are for stumps of *P. tremuloides* and *P. balsamifera*.

Stump size/distance relationships varied markedly among sites (Figure A5.5). A 2-factor ANOVA analysis found no significant effects on stump size of distance, site, or a distance x site interaction (Table 5.9).

Table 5.9 ANOVA table for effects of site and distance from water's edge on stump basal area

Source	SS	df	MS	F-ratio	p-value
distance	1.098	1	1.098	0.857	0.397
site	23.614	5	4.703	3.685	0.089
distance x site	6.408	5	1.282	0.464	0.802
error	347.819	126	2.76		

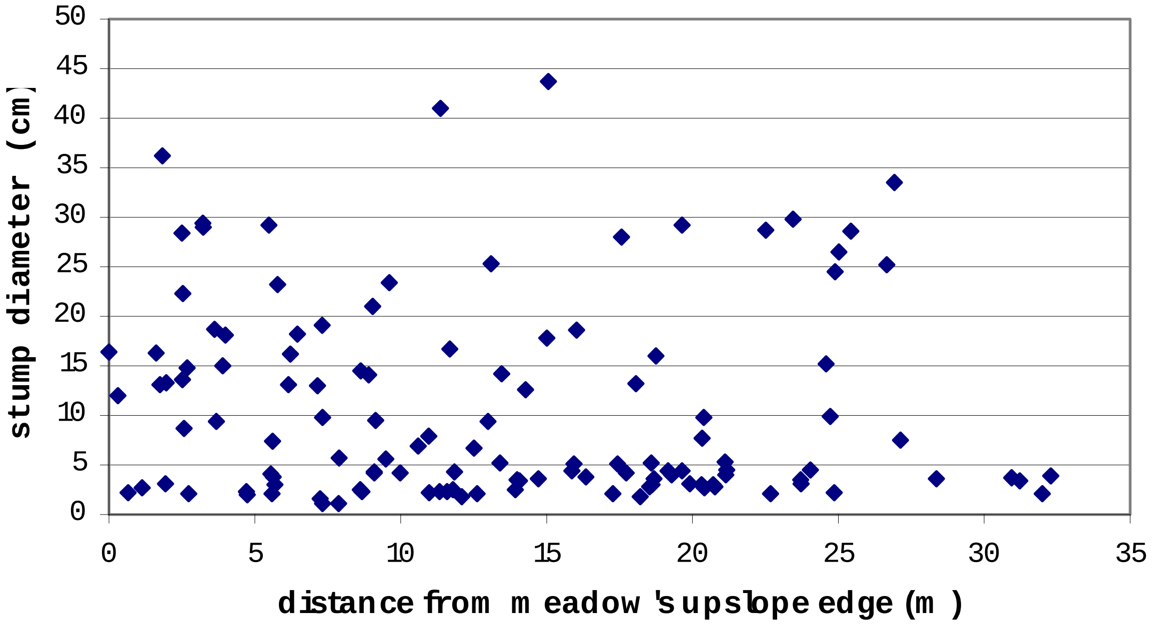
r2 = 0.337, n = 138

Stump diameters were measured at stump height, approximately 30 cm for all stumps > 1 cm dsh. Distance from water's edge is distance perpendicular from water's edge heading towards upland. Data are for stumps of *P. tremuloides* and *P. balsamifera*.

Using the upland edge of the meadow zone as the normal high water line, and therefore as the 0-distance mark beavers would travel in foraging, dramatically *reduced* the significance of the relationship between stump size and distance from water's edge and the explanatory power of the analysis (Figure 5.4). The regression equation for stump basal area with distance from meadow's edge was:

log(stump basal area) = -0.588 – 0.029 (distance) [n=123, r^2=0.016, p=0.161]

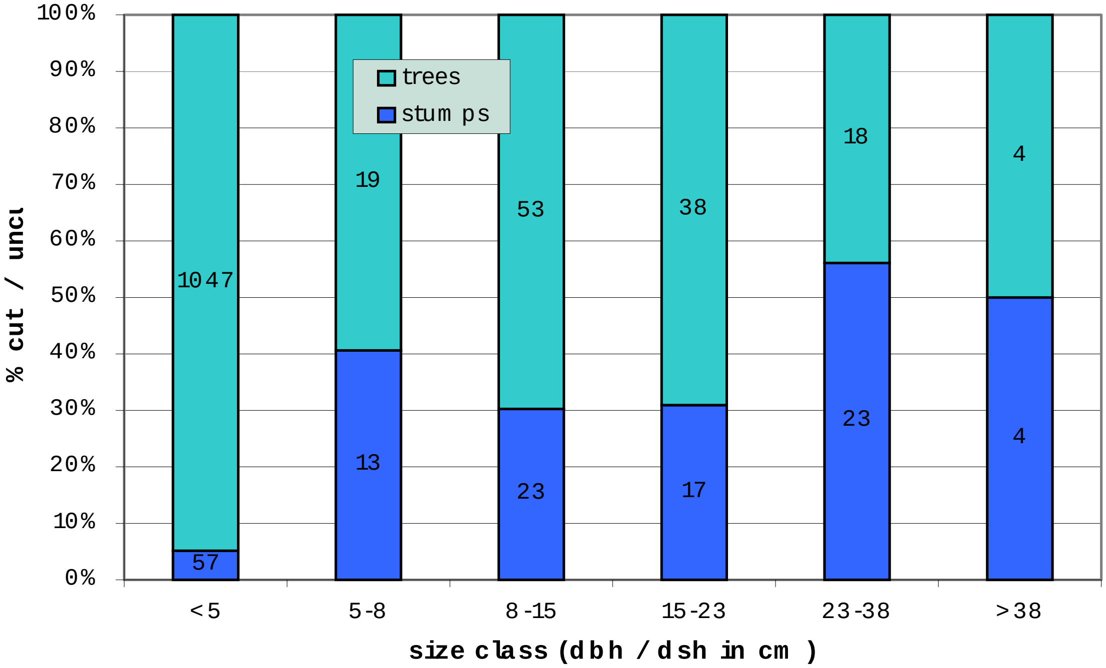
Figure 5.4 Relationship between stump diameter (cm) and distance from water's edge (m), using upslope edge of meadow zone as 0 distance, pooled across treatments and sites



Stump diameters were measured at stump height, approximately 30 cm for all *Populus* stumps > 1 cm dsh. Distance from water's edge is distance perpendicular from water's edge heading towards upland. Data are for stumps of *P. tremuloides* and *P. balsamifera*.

Overall, proportionally more trees were cut in the larger size classes compared to smaller size classes (Figure 5.5). This pattern is apparent at 5 of the 6 sites.

Figure 5.5 Proportion of total *Populus* basal area in each size class cut by beavers at active dams, pooled across sites



Stump diameters were measured at stump height, approximately 30 cm for all *Populus* stumps > 1 cm dsh. Distance from water's edge is distance perpendicular from water's edge heading towards upland. Data are for stumps of *P. tremuloides* and *P. balsamifera*. Proportion cut was calculated as (basal area stumps / basal area stumps + trees).

At each site, the highest proportion of trees were cut in the biggest size class available (Table 5.10); this pattern was particularly apparent at the two newest sites (Sites 9 and 13) where no trees in the smallest size classes had been cut (Figure A5.6).

Table 5.10 Number and proportion of *Populus* trees cut in each size class at each site, pooled across treatments

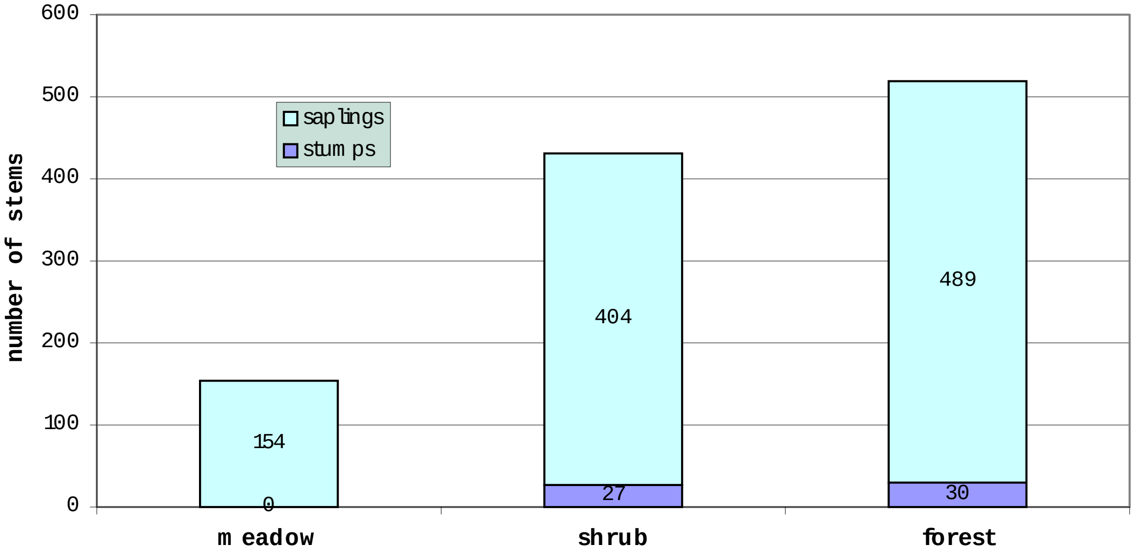
size class (cm dbh)	Site 4 cut	Site 4 uncut	prop cut	Site 5 cut	Site 5 uncut	prop cut	Site 7 cut	Site 7 uncut	prop cut	Site 9 cut	Site 9 uncut	prop cut	Site 12 cut	Site 12 uncut	prop cut	Site 13 cut	Site 13 uncut	prop cut	total cut	total uncut	prop cut
<5	39	215	0.15	1	13	0.07	15	455	0.03	0	7	0	2	300	0.01	0	57	0	57	1047	0.05
5-8	11	11	0.5	1	0	1	0	4	0	0	4	0	1	0	1	0	0	--	13	19	0.41
8-15	2	5	0.29	4	0	1	4	6	0.4	6	17	0.26	5	11	0.31	2	14	0.13	23	53	0.3
15-23	1	1	0.5	1	0	1	5	15	0.25	6	3	0.67	3	13	0.19	1	6	0.14	17	38	0.31
23-38	6	0	1	0	0	--	16	11	0.59	0	0	--	0	6	0	1	1	0.5	23	18	0.56
>38	0	1	0	0	0	--	2	1	0.67	0	0	--	2	2	0.5	0	0	--	4	4	0.5
Total	59	233	0.2	7	13	0.35	42	492	0.08	12	31	0.28	13	332	0.04	4	78	0.05	137	1179	0.1

Data are for stumps of *P. tremuloides* and *P. balsamifera*.

An higher proportion of trees in the larger size classes had been cut in the meadow and shrub zones than in the forest zone (Figure A5.7). Proportionally few saplings were cut in any zone (Figure 5.6).

Figure 5.6 Count of *Populus* stumps and trees in the sapling size class (< 5 cm dbh) for each vegetation zone, pooled across treatments and sites

(count printed inside column)



Data are for *P. tremuloides* and *P. balsamifera* combined. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

3.5 Sapling Density

Sapling abundance varied markedly among sites (Table 5.11) and with forest composition (Table A5.5). There was no effect of treatment on the abundance of *Populus* saplings (aspen and poplar; p=0.463), conifer saplings (p=0.207), or the proportion of deciduous saplings (p=0.463). At the newest sites (Sites 9, 13) there were similar numbers of conifer saplings upstream and downstream whereas older sites (Sites 4, 5) had many more conifer saplings upstream.

Table 5.11 Number of saplings per treatment for each site

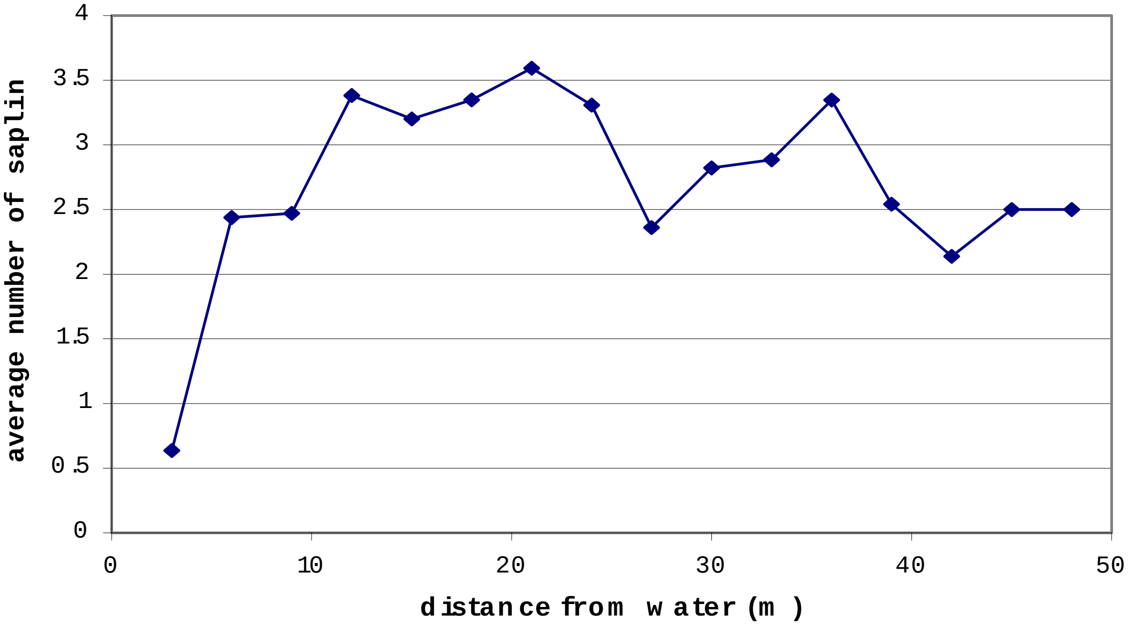
Site	**Aspen**		**Poplar**		**Spruce**		**Total Deciduous***		**Total Conifer^**	
	up	down	up	down	up	down	up	down	up	down
4	2	86	1	126	39	0	13	212	39	0
5	4	4	4	1	21	7	15	12	24	9
7	205	190	17	43	1	0	243	257	1	0
9	7	0	0	0	56	57	8	0	56	57
12	59	184	12	45	59	35	74	230	59	35
13	3	14	39	1	37	47	42	15	42	47
Total	280	478	73	216	213	146	395	726	221	148
Average	46.7	79.7	12.2	36.0	35.5	24.3	65.8	121.0	36.8	24.7

* aspen, poplar, paper birch
^ pine, fir, spruce

Treatment is upstream or downstream of dam.
Saplings are all stems < 5cm dbh.

For *Populus* saplings, there appeared to be an overall increase in abundance with distance from water's edge (Figure 5.7). This relationship was not statistically significant (p=0.315, n=96, r^2=0.011) and the regression model fit the data very poorly.

Figure 5.7 Average number of *Populus* saplings (<5 cm dbh) with distance from water's edge (m), pooled across sites.



Data are average sapling abundance per plot. Distance from water's edge is distance perpendicular from water's edge heading towards upland.

The relationship between sapling abundance and distance varied considerably among sites (Figure A5.8). An ANOVA analysis including the effects of site improved the fit considerably (r2 = 0.755, Table 5.12) and indicated a significant effect of site (p=0.000). There was no significant effect of distance (p=0.564) but there was a significant site x distance interaction (p=0.000).

Table 5.12 ANOVA table of effects of site and distance from water's edge on *Populus* sapling abundance

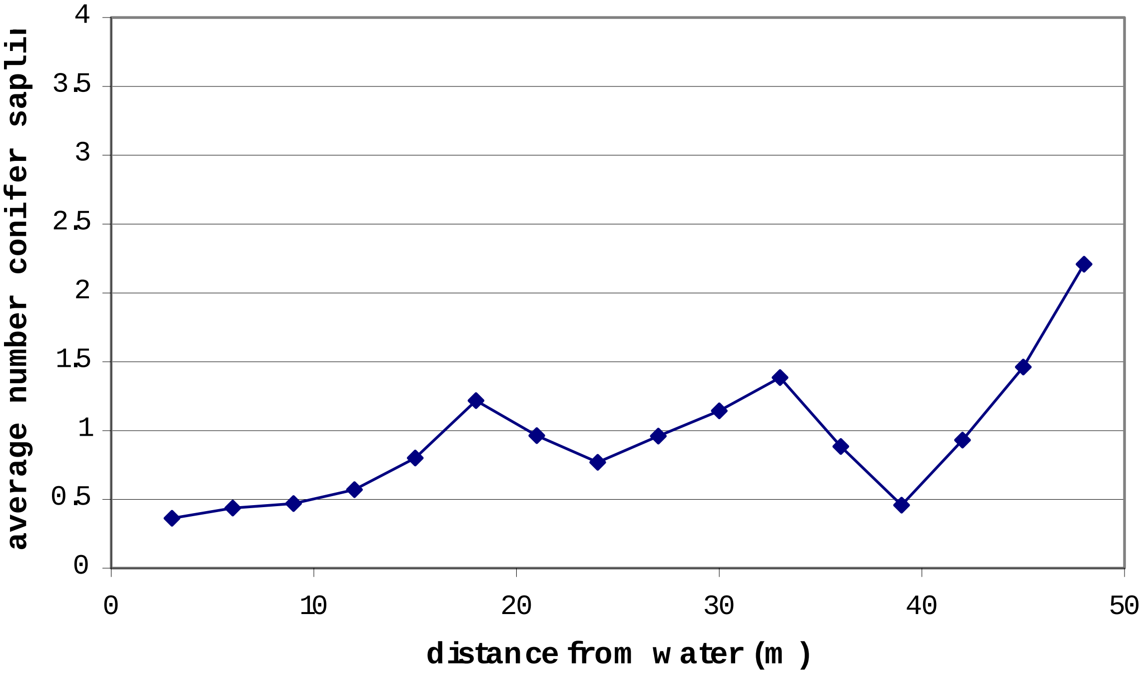
Source	SS	df	MS	F-ratio	p-value
distance	5.075	1	5.075	0.381	0.564
site	70.77	5	14.154	10.307	*0.000*
distance x site	66.552	5	13.31	9.693	*0.000*
error	115.351	84	1.373		

r2 = 0.755, n = 96

'Populus' is *P. tremuloides* and *P. balsamifera* combined. Saplings are all stems < 5 cm dbh. Distance from water's edge is distance perpendicular from water's edge heading towards upland, using plot as a proxy distance measurement. Data used were average per plot sapling abundance.

Conifer sapling abundance increased slightly with distance from water's edge (Figure 5.8). There was a significant effect of site (p=0.000) and distance (p=0.033), and a significant site x distance interaction (p=0.000)(Table 5.13, Figure A5.9).

Figure 5.8 Average number of conifer saplings (<5 cm dbh) with distance from water's edge, pooled across treatments and sites



Data are average sapling abundance per plot. Distance from water's edge is distance perpendicular from water's edge heading towards upland.

Table 5.13 Results of ANOVA test for effects of site and distance from water's edge on conifer sapling abundance, pooled across treatments

Source	SS	df	MS	F-ratio	p-value
distance	21.152	1	21.152	8.553	*0.033*
site	15.778	5	3.156	7.271	*0.000*
distance x site	12.366	5	2.473	5.699	*0.000*
error	36.453	84	0.434		

r2 = 0.729, n = 96

Saplings are all stems < 5 cm dbh. Distance from water's edge is distance perpendicular from water's edge heading towards upland, using plot as a proxy distance measurement. Data used were average per plot sapling abundance.

Sapling abundance varied among vegetation zones for both *Populus* and conifer species. Most saplings were concentrated in the shrub and forest zones and there were proportionally few saplings in the meadow zone (Table 5.14, Table 5.15).

Table 5.14 Proportion of *Populus* saplings in each vegetation zone, compared to availability of zone, at active beaver dams

Site	meadow		shrub		forest	
	prop saplings	prop zone	prop saplings	prop zone	prop saplings	prop zone
4	3.7%	51.0%	61.4%	36.5%	34.9%	12.5%
5	15.4%	41.7%	69.2%	17.7%	15.4%	40.6%
7	2.6%	15.6%	31.4%	35.4%	65.9%	49.0%
9	0.0%	3.1%	0.0%	3.1%	100.0%	93.8%
12	44.0%	31.3%	39.0%	27.1%	17.0%	41.7%
13	0.0%	10.4%	5.3%	4.2%	94.7%	85.4%
Average	**11.0%**	**26.4%**	**34.4%**	**25.5%**	**54.7%**	**53.8%**

'*Populus*' is *P. tremuloides* and *P. balsamifera* combined. Saplings are all stems < 5 cm dbh. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges. Proportion of saplings is the proportion of all *Populus* saplings measured at that site that were in that vegetation zone. Proportion zone is the proportion of the site that in that zone, calculated as (# plots in zone / total # plots at site). Data were pooled across transects and treatments within each site.

Table 5.15 Proportion of conifer saplings in each vegetation zone, compared to availability of zone, at active beaver dams

Site	meadow		shrub		forest	
	prop saplings	prop zone	prop saplings	prop zone	prop saplings	prop zone
4	48.7%	51.0%	12.8%	36.5%	38.5%	12.5%
5	24.2%	41.7%	33.3%	17.7%	42.4%	40.6%
7	0.0%	15.6%	100.0%	35.4%	0.0%	49.0%
9	0.9%	3.1%	0.0%	3.1%	99.1%	93.8%
12	2.1%	31.3%	20.2%	27.1%	77.7%	41.7%
13	0.0%	10.4%	2.2%	4.2%	97.8%	85.4%
Average	**12.7%**	**26.4%**	**28.1%**	**25.5%**	**59.2%**	**53.8%**

Saplings are all stems < 5 cm dbh. Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges. Proportion of saplings is the proportion of all *Populus* saplings measured at that site that were in that vegetation zone. Proportion zone is the proportion of the site that in that zone, calculated as (# plots in zone / total # plots at site). Data were pooled across transects and treatments within each site.

3.6 Importance Values

At all sites, the effect of beaver browsing was to decrease the importance of *Populus* (p=0.028) and increase the importance of conifers (p=0.028)(Table 5.16). This change was particularly apparent at sites with heavy browsing (sites 4 and 5) or with a very small conifer component (site 7). The newest sites (sites 9 and 13) had the lowest % change in conifer importance value. The importance value of *Populus* was not significantly different with treatment (p=0.225). The importance value of conifers was higher upstream than downstream at 5 of the 6 sites (Table 5.17) but the difference was not statistically significant (p=0.116).

Table 5.16 Importance values for *Populus* and conifers before and after beaver browsing at active beaver dams

	POPULUS									
	pre-browse				post-browse					
site	RF	RD	RB	*IV*	RF	RD	RB	*IV*	change in IV	% change in IV
4	13.54	50.66	57.01	*40.40*	7.29	56.25	29.66	*31.07*	**-9.34**	**-23.1**
5	7.29	2.59	4.16	*4.68*	0.00	0.00	0.00	*0.00*	**-4.68**	**-100**
7	16.67	94.44	99.57	*70.23*	9.38	94.87	99.32	*67.86*	**-2.37**	**-3.4**
9	12.50	15.86	21.48	*16.61*	10.42	11.21	12.70	*11.44*	**-5.17**	**-31.3**
12	11.46	84.91	77.90	*58.09*	10.42	82.05	71.27	*54.58*	**-3.51**	**-6.0**
13	10.42	9.12	16.25	*11.93*	8.33	8.14	13.63	*10.03*	**-1.90**	**-15.9**

	CONIFER									
	pre-browse				post-browse					
site	RF	RD	RB	*IV*	RF	RD	RB	*IV*	change in IV	% change in IV
4	4.17	8.55	40.32	*17.68*	4.17	40.63	69.61	*38.13*	**20.45**	**+115.7**
5	11.46	27.04	92.38	*43.62*	11.46	100.00	100.00	*70.49*	**26.86**	**+61.6**
7	1.04	1.11	0.19	*0.78*	1.04	2.56	0.42	*1.34*	**0.56**	**+71.8**
9	16.67	81.50	75.64	*57.94*	16.67	86.45	84.12	*62.41*	**4.48**	**+7.7**
12	4.17	7.55	21.33	*11.02*	4.17	10.26	27.74	*14.05*	**3.04**	**+27.6**
13	16.67	86.13	82.87	*61.89*	16.67	90.70	85.78	*64.38*	**2.49**	**+4.0**

'*Populus*' is *P. tremuloides* and *P. balsamifera* combined. Data were pooled across treatments within each site.

IV of species x = (RF + RD + RB) / 3, where

RF = relative frequency of species x,

RD = relative density of species x,

RB = relative basal area of species x (see Methods for calculation details)

'Pre-browse' is reconstructed stand before beaver browsing, calculated as stumps + trees.

Table 5.17 Importance values for *Populus* and conifers per treatment at active beaver dams, after beaver browsing

	POPULUS								
	upstream				**downstream**				
site	**RF**	**RD**	**RB**	***IV***	**RF**	**RD**	**RB**	***IV***	**difference in IV***
4	0.00	0.00	0.00	*0.00*	12.50	94.74	97.61	*68.28*	**68.28**
5	0.00	0.00	0.00	*0.00*	0.00	0.00	0.00	*0.00*	**0.00**
7	14.58	95.24	99.24	*69.69*	13.54	94.44	99.42	*69.14*	**-0.55**
9	3.13	5.88	4.91	*4.64*	11.46	16.07	23.38	*16.97*	**12.33**
12	15.63	75.00	55.14	*48.59*	13.54	93.33	98.95	*68.61*	**20.02**
13	10.42	15.31	18.58	*14.77*	4.17	3.75	8.77	*5.56*	**-9.21**

	CONIFER								
	upstream				**downstream**				
site	**RF**	**RD**	**RB**	***IV***	**RF**	**RD**	**RB**	***IV***	**difference in IV**
4	4.17	100.0	100.0	*68.06*	0.00	0.00	0.00	*0.00*	**-68.06**
5	28.13	100.0	100.0	*76.04*	16.67	100.00	100.00	*72.22*	**-3.82**
7	1.04	4.76	0.76	*2.19*	0.00	0.00	0.00	*0.00*	**-2.19**
9	41.67	92.16	93.13	*75.65*	36.46	81.25	71.79	*63.16*	**-12.49**
12	4.17	16.67	43.91	*21.58*	0.00	0.00	0.00	*0.00*	**-21.58**
13	40.63	84.69	81.42	*68.91*	43.75	94.38	90.05	*76.06*	**7.15**

* downstream IV - upstream IV

Treatment is upstream of downstream of beaver dam.
'*Populus*' is *P. tremuloides* and *P. balsamifera* combined.
IV of species x = (RF + RD + RB) / 3, where
RF = relative frequency of species x,
RD = relative density of species x,
RB = relative basal area of species x (see Methods for calculation details)
'Pre-browse' is reconstructed stand before beaver browsing, calculated as stumps + trees.

4 DISCUSSION

4.1 Beaver effects on riparian structure

Beaver dams have the obvious effect of raising surface water levels and creating ponds. Dams also raise the water table adjacent to and upstream of the dam and pond (Lowry 1993, Meentemeyer & Butler 1999); in some lowland situations this raised water table can extend for more than 40 m into the floodplain (Lowry 1993). Beaver dam effects on hydrology are complex and highly variable, however, depending on such factors as topography (Woo & Waddington 1990), whether the pond occurs as part of a sequence of dams, and dam spacing within a sequence (Gurnell 1998). These changes to water level can lead to tree death or increased growth, depending on topography and species. Species that can tolerate some degree of root flooding (such as black spruce and poplar) may survive upstream where species requiring well-drained soils (white spruce, aspen, pine) may be killed or experience severely reduced growth. In boreal Scandinavia it is common practice to install drainage ditches to improve growth in spruce forests (Stoeckeler 1963), an analogue effect of the increased growth observed downslope when roads or pipelines block wetland flows and lower downslope water tables (Jeglum 1975, Boelter & Close 1964).

In this study, snag abundance was not significantly higher upstream than downstream although 4 out of 6 sites did have more snags upstream. These results imply that there is likely an effect of beaver flooding on riparian forest structure, although it was not detected statistically (likely due to the small sample size). Tree death due to changes in water table is highly species-dependent (Green 1947, Hosner 1960, Landhäusser et al. 2003) and may also depend on length of flooding time (Landhäusser et al. 2003), and, at least for *Populus* species, on tree size and/or age (Rood & Mahoney 1990). The lack of upstream / downstream patterns of snag abundance for the different species supports the work of other researchers who have found that individual tree survival is most affected by microsite factors (Stoeckeler 1963, MacDonald & Yin 1999). The complexity of interacting factors may obscure overall patterns of tree death due to beaver flooding.

At the beaver dams in my study, tree size was not statistically different upstream and downstream, although there seemed to be an overall occurrence of smaller *Populus* trees and larger spruce trees upstream than downstream. Without an analysis of pre- and post-dam tree growth patterns, it is difficult to interpret these findings, especially in light of potential confounding effects of selective foraging and competitive release (see discussion below). Moreover, for spruce in peatlands, growth rate response to water table changes is strongly influenced by microsite factors (Lawrence 1952, MacDonald & Yin 1999). Overall, it seems reasonable to conclude that beaver-caused changes to hydrology may be affecting riparian forest structure in patterns too complex and site-specific to be elucidated by this study.

Effects of beaver foraging on riparian structure have been well-studied in eastern North America. For the most part, results of this study are similar to what is known of beaver foraging behaviour. In the boreal mixedwood forest, beavers seem to be mostly harvesting mature *Populus* trees whereas in eastern North America, they concentrate on smaller willows, alder, and other deciduous species (e.g. Donkor & Fryxell 1999, 2000), and use a much greater variety of shrub species than my study, where only *Salix* sp. were cut. Among tree species, *Populus* were used almost exclusively but these were also most abundant, and are known to be preferred over paper birch (Donkor & Fryxell 1999), the only other deciduous tree species available. Conifer species were essentially never used. Beaver foraging significantly lowered the relative importance of *Populus* species and, through avoidance, increased that of conifers. This change not only affects habitat availability but also, over time, may change soil properties (such as acidity and nutrient levels) and alter regeneration dynamics, through changing litter species.

At each site, beavers selected the largest trees available – a greater proportion of available trees were cut in larger size classes. This pattern is particularly apparent at the two new sites (sites 9 and 13). Overall very few saplings (<5 cm dbh) were ever cut (although sapling use may be underestimated by rapid decay of small stumps). All of these results are consistent with most other studies of beaver foraging (e.g. Johnston & Naiman 1990a, Jenkins 1980, but see Hall 1960). Beavers are considered central place foragers (Schoener 1979), concentrating more foraging effort and harvesting a wider range of tree species and sizes near the edges of ponds. The size of trees felled typically decreases with distance (Jenkins 1980, Pinkowski 1983) and with distance, beavers become increasingly selective of tree species (Fryxell & Doucet 1991) and size (Jenkins 1975, Jenkins 1980). The number of cut stems also declines sharply with distance (Hall 1960, Donkor & Fryxell 1999, Barnes & Mallik 2001). In this study, stump size decreased with distance from water's edge, a finding consistent with optimal central foraging theory as applied to beavers (Schoener 1979), but this relationship was surprisingly weak, especially in light of the strong relationship reported in other studies. Based on his studies of size- and distance-selection, Jenkins (1975, 1980) concluded that selection and use depend not only on species and size (jointly) but also on distance, availability, and vary between sites and colonies. These findings led him to speculate that size-selection for highly preferred species – such as *Populus* sp. – is only manifested at relatively large distances (Jenkins 1980). In my study, it is probable that a size-distance relationship in tree use was obscured by the variability in riparian forest composition among sites, since both species- and size-selection also depend on relative availability of different forage species (Pearson 1960). Moreover, I was unable to distinguish between aspen and poplar stumps. Aspen and poplar are distributed differently along the moisture gradient of riparian zones, with poplar typically more abundant closer to water's edge and aspen increasing further upslope (Zasada & Phipps 1990, Perala 1990, Strong 1992). Species, size, and distance selection may therefore have been confounded by species' responses to such edaphic gradients (as found, for example, by Donkor & Fryxell 2000).

4.2 Beaver effects on riparian succession

Studies of herbivores in a variety of ecosystems have demonstrated their ability to alter plant community composition through selective foraging and changes to nutrient cycling (for good reviews see Huntly 1991, and Adler et al. 2001). In some situations, these changes can also, over long time periods, affect succession pathways. In North American forests, beavers are the only species other than humans that can fell whole trees and thus have an immediate effect on the overstory. At my study sites, beaver effects on riparian succession appear to be happening in two distinct patch types: the zone closest to water's edge, which is converted to early successional meadow and shrub communities; and the forest zone, where removing deciduous trees increased the relative importance of conifers, creating stands that more closely resemble later successional stages (where conifers dominate).

The presence of large stumps and absence of conifer trees in the current meadow and shrub zones indicates that prior to beaver foraging, these patches were mature *Populus* forest. One interesting question is whether these areas will develop into forests, or if beaver activity will maintain them as early successional habitat. Long-term air photo studies indicate that beaver-created meadow and shrub riparian patches may last for decades or longer and in fact, suggest that once a forest is disturbed by beaver, it will not return to original forest (Rémillard et al. 1987, Johnston & Naiman 1990c), at least within the 40 or 50 year timeframe for which we have aerial photographs.

Maintenance of early succession habitat adjacent to the shoreline could occur due to restrictions at two levels: recruitment, or sapling survival. At my sites few saplings were browsed in any zone. Shifting riparian succession dynamics must therefore be due to factors other than beaver browsing. There were proportionally few saplings in the meadow zone, compared to studies of clear-cuts where open edges were characterised by heavy suckering of aspen and poplar (Harper & MacDonald 2002). The air photo analysis (Chapter 5) indicated that these meadow zones were formerly flooded sections of the pond that had drained after several consecutive drought years. Flooding can alter soil properties, killing soil mycorrhizae critical for spruce germination and seedling survival and thus restricting tree invasion even after dam removal and pond draining (Wilde et al. 1950, Terwillegar & Pastor 1999). At my study sites, there was no difference in sapling density upstream and downstream, implying that neither changes to water table nor residual effects of soil flooding are the factor limiting sapling recruitment, or, perhaps, that their effects were overshadowed by another agent affecting both up- and downstream areas. Meadow zones had heavy sedge and grass cover, as well as a thick layer of thatch from previous years' growth. Most boreal tree species need mineral soil to germinate (Greene 1999, Frank 1990, Lotan & Critchfield 1990, Nienstaedt & Zasada 1990, Perala 1990, Rudolph & Laidly 1990, Viereck & Johnston 1990, Zasada & Phipps

1990) and although *Populus* species reproduce largely by vegetative suckering from roots (Moss 1932, Perala 1990, Zasada & Phipps 1990), inundation kills the roots (DeByle & Winokur 1985); *Populus* reinvasion of drained beaver meadows is therefore a very slow process, dependent upon growth of roots from trees adjacent to the meadow (DeByle & Winokur 1985, Greene 1999). In addition, competition with grasses significantly reduces *Populus* suckering and sapling growth (Landhäusser & Lieffers 1998) and it is reasonable to presume that the grass cover could exclude conifer seedlings as well (Lieffers et al. 1993).

In the forest zone, beaver activity may be acting at two levels to shift the vegetation composition towards a later seral stage: first, by removing mature aspen and increasing the importance of conifers; and secondly, by affecting advance regeneration and understory dynamics to hasten the conversion to, and subsequently to maintain, the site as a spruce stand. Beaver foraging certainly led to significant reduction in density and relative importance of *Populus* at my study sites, which could lead to increased growth of understory conifers through competitive release. Aspen does not regenerate well under closed canopy (Perala 1990, Navratil et al. 1991) and even considering its ability to reproduce via suckers, supporting saplings through the connected root system, older aspen do not sucker as well as young ones (DeByle & Winokur 1985) and there is little evidence that these suckers survive in the relative shade of a closed canopy (Cumming et al. 2000, Navratil et al. 1991). Spruce, on the other hand, does regenerate well under canopy, and the beaver-mediated change in overstory composition may also increase conifer recruitment since conifers regenerate much better on conifer litter than hardwood leaf litter (Greene 1999, Nienstaedt & Zasada 1990).

Sapling recruitment by preferred forage species at beaver sites is negatively related to foraging pressure and according to central-place foraging theory, sapling density of preferred species should increase with distance from water's edge (Jenkins 1980, Donkor & Fryxell 1999). Sapling densities did not change significantly with distance at my sites; while these results may be due in part to the variability among sites, they also support my finding that beavers are not browsing on *Populus* saplings. The relative density of deciduous and coniferous saplings also did not change with distance, implying that foraging pressure has little effect on sapling recruitment.

Without comparison to non-beaver influenced areas, and a more detailed analysis of seedling recruitment and sapling success, I hesitate to infer further mechanisms of beavers' role in altering riparian succession in boreal mixedwood forests. Rowe (1961) argues that succession theory does not apply to the boreal mixedwood, where interacting disturbance regimes and variable site conditions lead to several 'climax' forest communities, "some transitional, some relatively persistent". Regeneration patterns at beaver sites typically show great diversity, both before and after abandonment (Donkor & Fryxell 1999, Barnes & Mallik 2001). The complex and non-linear succession pathways of both beaver sites (Barnes & Dibble 1988, Rémillard et al. 1987, Syphard & Garcia 2001) and the surrounding forest (Rowe 1961, Pojar 1996) may preclude any generalizations about the effects of beavers on riparian succession in boreal mixedwood ecosystems. Despite these caveats, my study sites clearly showed a shift from deciduous to conifer – a change seen in both the overstory (as beavers fell mature *Populus* trees) and in regeneration dynamics (as beavers shift the relative abundance of deciduous and conifer saplings).

4.3 Temporal dynamics of beaver effects

The large age range of the beaver dams in this study provided some interesting insights into temporal changes at beaver ponds, although the small sample size precludes statistical analysis. Logically, beaver effects on riparian succession take time to manifest. These gradual changes could be inferred from sites of different ages in my study. The new sites had very similar conifer sapling density up- and downstream of the dam, whereas at older sites there were many conifer saplings upstream and almost none downstream. Older sites also had a higher percent change in conifer importance value pre- and post-browse.

It is not surprising that newer dams have fewer stumps than older ones. What is interesting is that at newer sites, the range of stump size is smaller and the average stump size is bigger – i.e., beavers are removing larger trees first. This finding is predicted according to optimal foraging theory as applied to beavers (Schoener 1979), and beaver size-selectivity reported in other studies (Jenkins 1975) but temporal change in beaver foraging has rarely been explicitly addressed in the literature.

Many of the older dams were in chains of dams where the downstream area had previously been an active pond. The newer dams, in contrast, were either single or the biggest and most-established dam in a forming chain. Results from both a chronosequence analysis of these sites (Chapter 5, this thesis) and from other researchers (Johnston & Naiman 1990b, Townsend & Butler 1996) show that the first dam in a sequence also tends to be the most permanent. One impact of the 'chain effect' at older dams is the extreme variability of meadow and shrub zone widths, and of the relative widths of these zones upstream and downstream of the dam (presumably partly due to differences in pre-draining pond size). The newest sites had much smaller meadow and shrub zones than older ones, and smaller differences in zone width between upstream and downstream. This conclusion is supported by air photo time-sequence studies in other areas, that have found that these beaver-created meadow / shrub patches increase over time, and are very long-lived (Rémillard et al. 1987, Johnston & Naiman 1990a).

Overall, these differences between dams of differing ages not only supports conclusions that beavers affect riparian succession dynamics, but also imply that whatever combination of flooding and foraging creates and maintains non-forest riparian zones, and affects vegetation succession, is cumulative over time.

Chapter 6 Conclusions and Recommendations

1 IMPACTS OF ROAD CROSSINGS ON STREAMS IN NORTHEASTERN ALBERTA BOREAL PLAIN

This study did not detect strong vegetation responses that would indicate hydrological impacts from road crossings on defined streams in the boreal plains of northeastern Alberta. The small sample size and big among-site variability reduced power to detect any significant effects. Despite these study limitations, my opinion, based on my observational *gestalt* of both the sample sites and other road crossings in the study area, is that these road crossings do cause significant flow interruptions, through their interaction with beavers. Due to this interaction, however, this project was a study of the road-plus-beaver unit without comparison to road crossings that had not been influenced by beaver activity.

Both the field survey and the chronological analyses in this project highlight the spatial and temporal variability of beaver effects, the shifting of dam location and abundance along stream corridors and the unpredictable longevity and impacts of dams (not to suggest that dam life-span and location change capriciously, but rather that we do not understand the factors involved in sufficient detail to predict the changes). In comparison, road crossings are permanent, *potential* interruption points due to their susceptibility to blocking by beavers. Roadbeds and their culverts are clearly attractive to beavers as "pinch points" in waterways where the payoff in area-flooded can be substantial for the effort required to plug just the culvert. Predictably, the response of road managers is to kill or relocate the beavers. Both the field study and the air photo chronosequence analyses showed that these crossings are not permanently dammed (although they may be dammed frequently for short periods). Although attractive to beavers, therefore, riparian areas near road crossings may experience lesser beaver impact than other locations along the riparian corridor. The perpetual removal of beavers may reduce the tree felling and flooding effects in riparian zones adjacent to roadways compared to other areas – the riparian zones adjacent to roads could serve as beaver-free riparian reserves. Over time, this “reduced beaver zone” effect may create areas of non-beaver-influenced riparian areas in otherwise heavily-altered watersheds. Some aspects of this line of speculation are being addressed in current corollary studies being conducted by Nadele Flynn and Kerri Lappin through the AME Project.

The boreal plains have large areas of peatlands and forested wetlands. In these areas, beaver dams can create an interruption in shallow surface groundwater movement, creating surface ponds where there is otherwise no apparent surface water (*personal observation*; Rebertus 1986 and Ray et al. 2001 both report this phenomenon in boreal areas of eastern North America). Roads can also block these slow-flowing wetlands (Jeglum 1975), especially when crossings are not designed with appropriate culvert numbers and placement. Aerial photographs that show zones of altered riparian areas up- and downstream of road crossings may be showing this effect. I believe that hydrological interruption due to roads in boreal Alberta is more important in these peatland situations than at the defined stream channels examined in this study.

2 BEAVERS AS A KEYSTONE SPECIES

The chronosequence analysis of beaver-influenced streams, observed through a time of expanding beaver population, revealed the importance of beaver in structuring wetlands and riparian habitats in the boreal mixedwood. This study showed that beavers in the boreal mixedwood of northeastern Alberta exert a considerable influence on the structure and relative availability of types of riparian areas. In a landscape devoid of beavers (early years of the photo sequence), there are few ponds, and narrow riparian areas, associated with the study streams. Beaver activity greatly increased the diversity of habitats, both aquatic and terrestrial, across the landscape, creating and maintaining habitat for a variety of plants and animals known to depend on riparian wetlands and a successional sequence of ponds. Thus, beavers may be the primary disturbance agent structuring riparian zones on low-order streams in the study area. In light of these impacts, and the fact that beaver-created wetlands are believed to provide crucial habitat for wetland-dependent species in boreal forests (Nummi 1992, Rempel et al. 1997), I propose that beavers be considered a *keystone species* modifying habitats in the boreal mixedwood forests of Alberta (sensu Power et al. 1996: a species whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance).

3 BEAVERS AND BUFFER MANAGEMENT

The results of this study challenge the buffer widths prescribed in Alberta's current Operating Ground Rules, which have not been based on ecological data from this area. Beaver flooding and foraging can remove most (or all) trees within 60 m or more of the unimpounded stream edge, and maintain these patches as meadow or shrub habitats for long periods of time. One implication of this finding is that Alberta's current riparian buffer prescriptions may be inadequate to meet the goals of habitat provision for riparian-dependent species. The ecology of small-order, headwater streams has been poorly studied compared to larger downstream networks, and their significance in channel networks has been underestimated (Gomi et al. 2002); their role in hydrologic, geomorphic, and biological processes is unknown in boreal mixedwood systems. Wider buffer strips could accommodate pond creation, while still retaining some surrounding forest structure for both beaver forage, and protecting aquatic systems from impacts of upland harvesting.

4 FURTHER EXPLORATIONS

4.1 Expansions of this study

This study was a preliminary examination of the potential rôle of beavers and roads (singly, and in concert) in structuring riparian habitats in the boreal mixedwood region. A detailed hydrological study could better address the original objective, which was to detect and quantify hydrological interruptions due to road crossings. Moreover, a larger sample size and reduced site variability – perhaps a stratified sampling design of different ages and types of roads – could help to clarify any underlying patterns that were obscured by variability among my sites.

Since my project was not designed to be an in-depth study of beaver habitat use, I was not able to answer some key questions about beaver impacts. Comparative studies of beaver-influenced to non-beaver-influenced areas would elucidate the proportion of landbase affected by beavers, and their relative impacts in different areas (e.g. beaver use of streams in different areas of a catchment, or a different order). In addition, a larger sample size of dams of a range of ages would clarify long-term and broad-scale effects, as would expanding the study scope to explore how beavers use different ponds in a chain, how foraging changes with longitudinal distance from the dam, and more detailed use-availability studies including shrub species.

4.2 Above and beyond

This study of beavers and road crossings was conducted under the ægis of the Adaptive Management Experiment Team, whose goals include developing alternative management strategies to ensure sustainable resource use in the boreal forest. There have been few evaluations of how successfully buffer strips conserve species and ecological processes in boreal mixedwood forests (Stelfox 1995, but see Machtans et al. 1996, Hannon et al. 2002 for two recent studies). A critical first step to improving our understanding and thus management policies for riparian areas should be preliminary studies of buffer width function and effectiveness for different species and management goals.

All landscape-level management planning must consider the connections between riparian areas and upland forests. Beaver habitat use may be affected by harvesting activities in the surrounding forest and along the stream corridor. For example, forest harvesting may change the availability of forage trees not only by removing mature aspen and poplar but also by creating patches of regenerating trees. Ten to fifteen years post-harvest, dense stands of aspen suckers on these cutblocks may be particularly appealing to beavers by providing a preferred size-class for both feeding and dam construction. My study sites were chosen to avoid nearby cutblocks. One critical line of enquiry for variable buffer planning would be an understanding of beaver use of cutblocks near water's edge and specifically of buffer strips themselves: If there is a cutblock with a conventional 30 m buffer strip, do beavers fell these trees as in other areas – or do they bypass these trees in favour of the adjacent regenerating cutblock? Will beavers utilise habitats where trees have been harvested right to the stream bank? How is this use affected by relative landscape availability of intact riparian areas, buffer strips, and cutblocks? These questions could be answered by studying streams harvested using an experimental series of variable-width buffers.

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Appendix 3.1 Details of photos used in chronosequence analysis

site	year	scale (1:)	project no.	AS	flight line	photo	details
4	1951	15 840	1951-83P	AS367	5502	165	SUPER XX
	1964	31 680	1964-83P	AS891	5501	183	B/W
	1967	31 680	1967-83P	AS971	5502	71	B/W
	1978	15 000	1978-050B 83P	AS1707	39	151	B/W PAN 2405
	1988	20 000	1988-101	AS3739	26	23	B/W PAN-150
	1992	15 000	1992-154	AS4335	2	76	IR 2424
	1997	15 000	1997-197	AS4881	2	24	B/W IR
	2000	20 000	2000-019	AS5109	1	134	BW DOUBLE
	2002	20 000	2002-046	AS5214	2	96	B/W Agfa-200
5	1951	15 840	1951-84B	AS 208		79	SUPER XX
	1965	31 680	1965-84B	AS907		71	IR 2424
	1973	21 120	1973-013	AS1232	27	64	PAN 2405
	1978	15 000	1978-053	1868	48	128	B/W IR-2424
	1985	10 000	S85-061	AS3196	8-W	132	PAN 2405
	1986	25 000	S1986-072	AS3025	9-W	43	PAN 2405
	1988	40 000	1988-214	AS3746	89	214	PAN 150
	1990	15 000	1990-149	AS4039	13	215	IR 2424
	1995	15 000	1995-095	AS4667	28	151	B/W IR
	1997	15 000	1997-132 W 5	AS4787	28	171	False Colour*
7	1951	15 840	1951-73M	AS356		75	SUPER XX
	1967	31 680	1967-73M	AS971		193	B/W
	1974	24 000	1974-167	AS1442	2	22	PAN 2405
	1978	15 000	1978-050A 73M	AS1755	43	180	B/W IR-2424
	1983	60 000	1983-143	AS2790	71	49	PAN 2405
	1990	40 000	1990-134A	AS4111	4	97	PAN 150
	1993	15 000	1993-175	AS4451	24A	88	IR 2424
	1998	20 000	1998-052	AS4925	8-W	243	False Colour*
	2000	30 000	2000-093	AS5143	48E	232	B/W A50
9	1951	15 840	1951-73M	AS314	5524	57	SUPER XX
	1961	31 680	1961-73M	AS799	5512	240	B/W
	1977	50 000	1977-108C 73M	AS1606	36	249	B/W PAN-2405
	1978	15 000	1978-050A 73M	AS1770	63	271	B/W IR-2424
	1979	25 000	S1979-013A	AS1829	9	246	PAN 2405
	1983	60 000	1983-143	AS2791	76	146	PAN 2405
	1991	40 000	1991-192	AS4202	76B	99	PAN 150
	1996	15 000	1996-131	AS4703	13E	57	B&W IR
	2002	20 000	2002-051	AS5229	1	8	B/W Agfa-200

Appendix 5.1 (cont'd) Details of photos used in chronosequence analysis

site	year	scale (1:)	project no.	AS	flight line	photo	details
13	1951	15 840	1951-84B	AS230	5620	111	SUPER XX
	1965	31 680	1965-84B	AS910		166	IR 2424
	1970	15 840	1970-210	AS1068	2	229	IR 2424
	1971	15 840	1971-066	AS1097	1	208	PAN 2405
	1972	12 000	1972-191	AS1293	17	300	PAN 2405
	1973	21 120	1973-013	AS1230	19	54	PAN 2405
	1978	15 000	1978-053	AS1863	38	125	B/W IR-2424
	1981	16 000	1981-175	AS2411	2	36	PAN 2405
	1989	20 000	1989-182	AS3931	1NW	127	PAN 150
	1991	20 000	1991-222	AS4175	2	35	PAN 150
	1995	15 000	1995-095	AS4665	18	22	B/W IR
	2001	20 000	2001-026	AS5202	1	104	B/W Agfa-200
	2002	20 000	2002-021	AS8413	1	120	B/W Agfa-200
14	1951	15 840	1951-84B	AS210	5628	79	SUPER XX
	1965	31 680	1965-84B	AS908		170	IR 2424
	1973	21 120	1973-013	AS1231	26	285	PAN 2405
	1978	15 000	1978-053	AS1867	47	270	B/W IR-2424
	1981	16 000	1981-175	AS2411	3	44	PAN 2405
	1982	6 000	1982-158	AS2668	2	233	IR 2424
	1988	40 000	1988-214	AS3746	89	96	PAN 150
	1990	15 000	1990-149	AS 4039	11	159	IR 2424
	1995	15 000	1995-095	AS 4667	27	82	B/W IR
	1997	15 000	1997-132 W 5	AS4787	27	89	False Colour*
	2001	20 000	2001-026	AS5200	1	145	B/W Agfa-200

Appendix 5.1 (cont'd) Details of photos used in chronosequence analysis

site	year	scale (1:)	project no.	AS	flight line	photo	details
15	1951	15 840	1951-83P	AS357	5506	95	SUPER XX
	1967	31 680	1967-83P	AS971	5503	120	B/W
	1975	31 680	1975-033 83P	AS1390	19	229	B/W PAN-2405
	1978	15 000	1978-050A 83P	AS1755	42	35	B/W IR-2424
	1980	15 000	1980-046	AS2135	1	176	PAN 2405
	1990	20 000	1990-133	AS4107	16	230	PAN & IR
	1991	20 000	1991-058	AS4149	1	147	IR 2424
	1993	15 000	1993-175	AS4451	23	43	IR 2424
	1998	15 000	1998-052	AS4894	5E	142	False Colour*
	1999	15 000	1999-113 83P	AS5058	25	209	False Colour*
	2000	20 000	2000-019	AS5109	4W	182	BW DOUBLE
	2002	20 000	2002-046	AS5214	4	116	B/W Agfa-200
16	1951	15 840	1951-83P	AS341	5513	42	SUPER XX
	1967	31 680	1967-83P	AS970		79	B/W
	1978	15 000	1978-050A 83P	AS1758	49	157	B/W IR-2424
	1979	20 000	1979-068 TARGET	AS1944		46	B/W
	1982	30 000	1982-090 83P	AS2639	77	210	B/W PAN-2405
	1992	20 000	1992-022 83P	AS4246	3	87	PAN 200
	1993	15 000	1993-175	AS4453	31	95	IR 2424
	1994	20 000	1994-020	AS4481	1	124	A 200
	1995	20 000	1995-058	AS4601	1	176	AGFA 200
	1998	20 000	1998-040	AS4926	2W	37	DOUBLE X
	2000	20 000	2000-022	AS5109	4E	238	BW DOUBLE
	2002	20 000	2002-046	AS5214	10	201	B/W Agfa-200

Appendix 3.2 Chronosequence of beaver activity at Site 4.

a) details of ærial photo analysis.

b) 2002 aerial photo of Site 4

c) 1978 aerial photo of Site 4

d) 1951 aerial photo of Site 4

Appendix 3.3 Chronosequence of beaver activity at Site 5.

a) details of ærial photo analysis.

b) 1997 aerial photo of Site 5

c) 1978 aerial photo of Site 5

d) 1951 aerial photo of Site 4

Appendix 3.4 Chronosequence of beaver activity at Site 7

a) details of ærial photo analysis.

b) 1998 aerial photo of Site 7

c) 1978 aerial photo of Site 7

d) 1951 aerial photo of Site 7

Appendix 3.5 Chronosequence of beaver activity at Site 9.

a) details of ærial photo analysis.

b) 2002 aerial photo of Site 9

c) 1977 aerial photo of Site 9

d) 1951 aerial photo of Site 9

Appendix 3.6 Chronosequence of beaver activity at Site 12.

a) details of ærial photo analysis.

b) 2000 aerial photo of Site 12

c) 1978 aerial photo of Site 12

d) 1951 aerial photo of Site 12

Appendix 3.7 Chronosequence of beaver activity at Site 13.

a) details of ærial photo analysis.

b) 2002 aerial photo of Site 13

c) 1978 aerial photo of Site 13

d) 1951 aerial photo of Site 13

Appendix 3.8 Chronosequence of beaver activity at Site 14 (road-only site).

a) details of ærial photo analysis.

b) 2001 aerial photo of Site 14

c) 1978 aerial photo of Site 14

d) 1951 aerial photo of Site 14

Appendix 3.9 Chronosequence of beaver activity at Site 15 (road-only site).

a) details of ærial photo analysis.

b) 2002 aerial photo of Site 15

c) 1978 aerial photo of Site 15

d) 1951 aerial photo of Site 15

Appendix 3.10 Chronosequence of beaver activity at Site 16 (road-only site).

a) details of ærial photo analysis.

b) 2002 aerial photo of Site 16

c) 1978 aerial photo of Site 16

Table A 4.1 Analysis of Variance Table - Split-plot design with blocks (sites) as random, and factors A (wetland type) and B (location) fixed

Table A4.2 Snag density (count per 100m²) per treatment at road crossings

Site	upstream		downstream	
	Populus	all species	*Populus*	all species
4	2.08	2.08	4.17	4.4
5	0.00	9.38	0.00	7.87
7	1.16	1.85	1.39	1.62
9	0.00	2.08	0.69	2.08
12	2.31	3.24	0.69	0.69
13	2.55	3.82	5.21	3.7
14	0.46	2.78	1.16	1.16
15	1.62	1.62	0.57	2.85
16	0.93	2.08	1.39	2.08
average	**1.23**	**3.21**	**1.70**	**2.94**

Snag densities were calculated pooling snags across transects within each treatment.
Populus category represents snags of *P. tremuloides* and *P. balsamifera*.

Table A4.3 Average tree basal area (m²) per treatment for *Populus*, spruce, all conifers, and all species at each road crossing site

Site	all species		*Populus*		Spruce		all conifer	
	up	down	up	down	up	down	up	down
4	0.012	0.013	0.012	0.013	.	.	.	.
5	0.014	0.013	.	0.006	0.008	0.012	0.025	0.027
7	0.034	0.029	0.034	0.029	.	.	.	.
9	0.014	0.020	0.008	0.011	0.065	0.039	0.072	0.050
12	0.037	0.034	0.037	0.034	.	.	.	.
13	0.026	0.020	0.023	0.015	0.028	0.026	0.028	0.033
14	0.014	0.016	0.015	0.014	0.011	0.017	0.026	0.037
15	0.011	0.017	0.011	0.017	.	.	.	.
16	0.013	0.014	0.010	0.008	0.014	0.013	0.087	0.049
Average	0.019	0.020	0.019	0.016	0.025	0.021	0.048	0.039

Treatment is upstream or downstream of road crossing.

Data presented are an average of all trees measured in each treatment (pooled across transects). *Populus* category incuded *P. tremuloides* and *P. balsamifera*.

Figure A4.1 Tree size class structure per treatment at road crossings, pooled across all sites

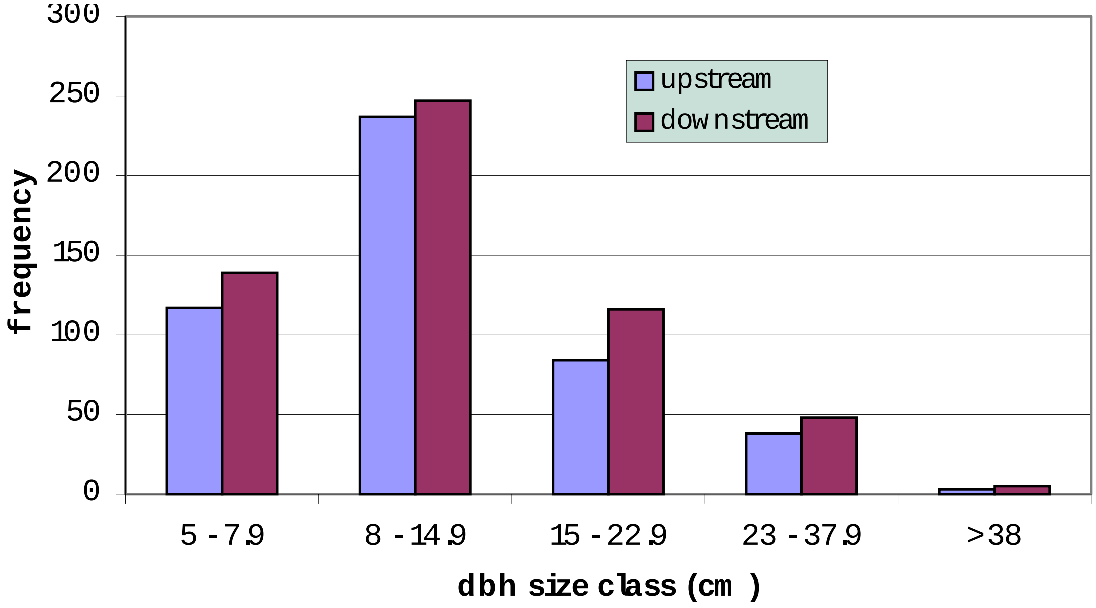


Figure A4.2 *Populus* tree size class structure per treatment at road crossings, pooled across all sites

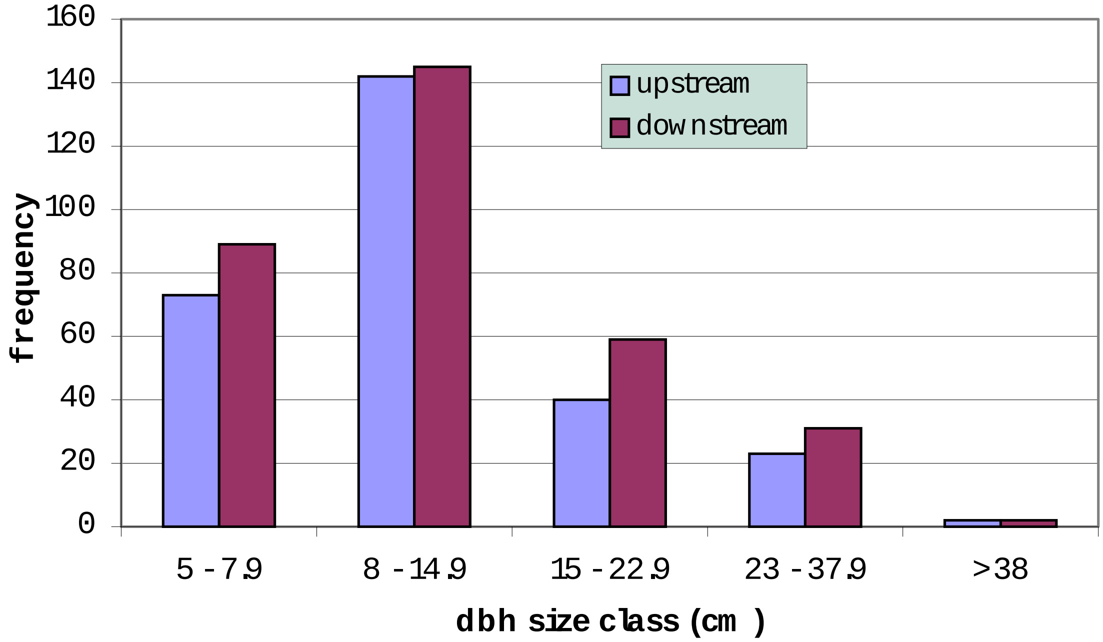


Figure A4.3 Spruce tree size class distribution per treatment at road crossings, pooled across all sites

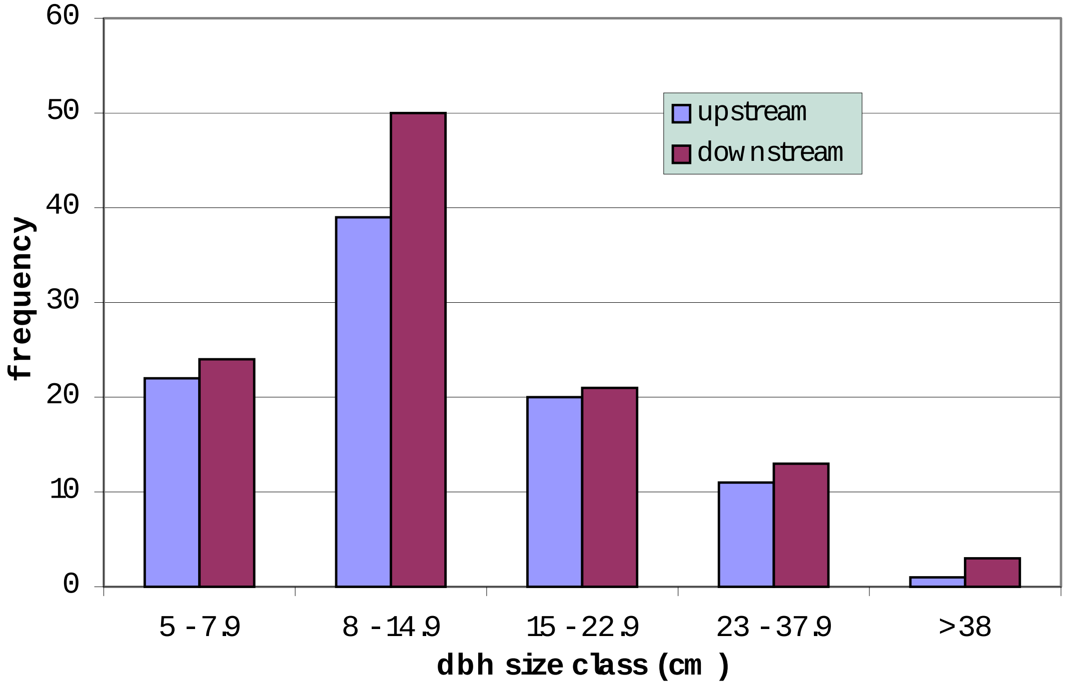


Table A4.4 Sapling density (count per $100m^2$) per treatment at road crossings

Site	all species		*Populus tremuloides*		*Populus balsamifera*		Spruce		total deciduous*		total conifer~	
	up	down	up	down	up	down	up	down	up	down	up	down
4	26.4	34.7	11.6	20.8	14.6	13.9	0.2	0.0	26.2	34.7	0.2	0.0
5	5.6	4.2	3.1	0.0	0.0	0.5	12.8	3.2	2.1	0.5	3.5	3.7
7	101.7	18.8	56.3	17.4	8.6	1.4	0.0	0.0	101.7	18.8	0.0	0.0
9	47.0	67.9	13.4	0.5	0.5	1.4	5.1	7.4	19.2	3.5	27.8	64.4
12	17.4	42.6	13.2	27.1	3.5	13.2	0.7	1.6	16.7	41.0	0.7	1.6
13	42.3	26.2	16.0	10.6	9.4	5.6	0.7	5.6	25.3	16.2	17.0	10.0
14	11.1	7.6	1.9	1.6	2.8	0.7	5.8	5.3	4.6	2.3	6.5	5.3
15	49.8	60.7	12.5	47.6	27.3	12.3	0.0	0.0	49.8	60.7	0.0	0.0
16	12.5	19.5	0.9	0.7	2.5	0.0	9.0	18.8	3.5	0.7	9.0	18.8
Average	34.9	31.4	14.3	14.0	7.7	5.4	3.8	4.7	27.7	19.8	7.2	11.5

* 'total deciduous' includes paper birch saplings

~ 'total conifer' includes balsam fir and pine saplings.

Data are pooled across transects within each treatment . Treatments are upstream or downstream of road crossing.

Table A4.5 Snag density (count / 100m^2) per treatment at each beaver dam and road crossing

Site	beaver dams			road crossings		
	up	down	total	up	down	total
4	1.39	2.08	0.93	2.08	4.17	3.13
5	0.00	0.00	0.00	0.00	0.00	0.00
7	1.16	1.16	1.74	1.16	1.39	1.27
9	0.69	0.00	1.27	0.00	0.69	0.35
12	2.08	2.31	2.20	2.31	0.69	1.50
13	4.63	3.82	3.70	3.82	3.47	3.61
Average	1.66	1.56	1.64	1.56	1.74	1.64

Data are for all species, pooled across transects within each treatment.

Treatments are upstream or downstream at each beaver dam or road crossing.

Figure A4.4 Visual representation of vegetation zones at road crossing and beaver dam at each site.

Zone widths have been extrapolated between transects sampled. Zones were defined for each plot using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

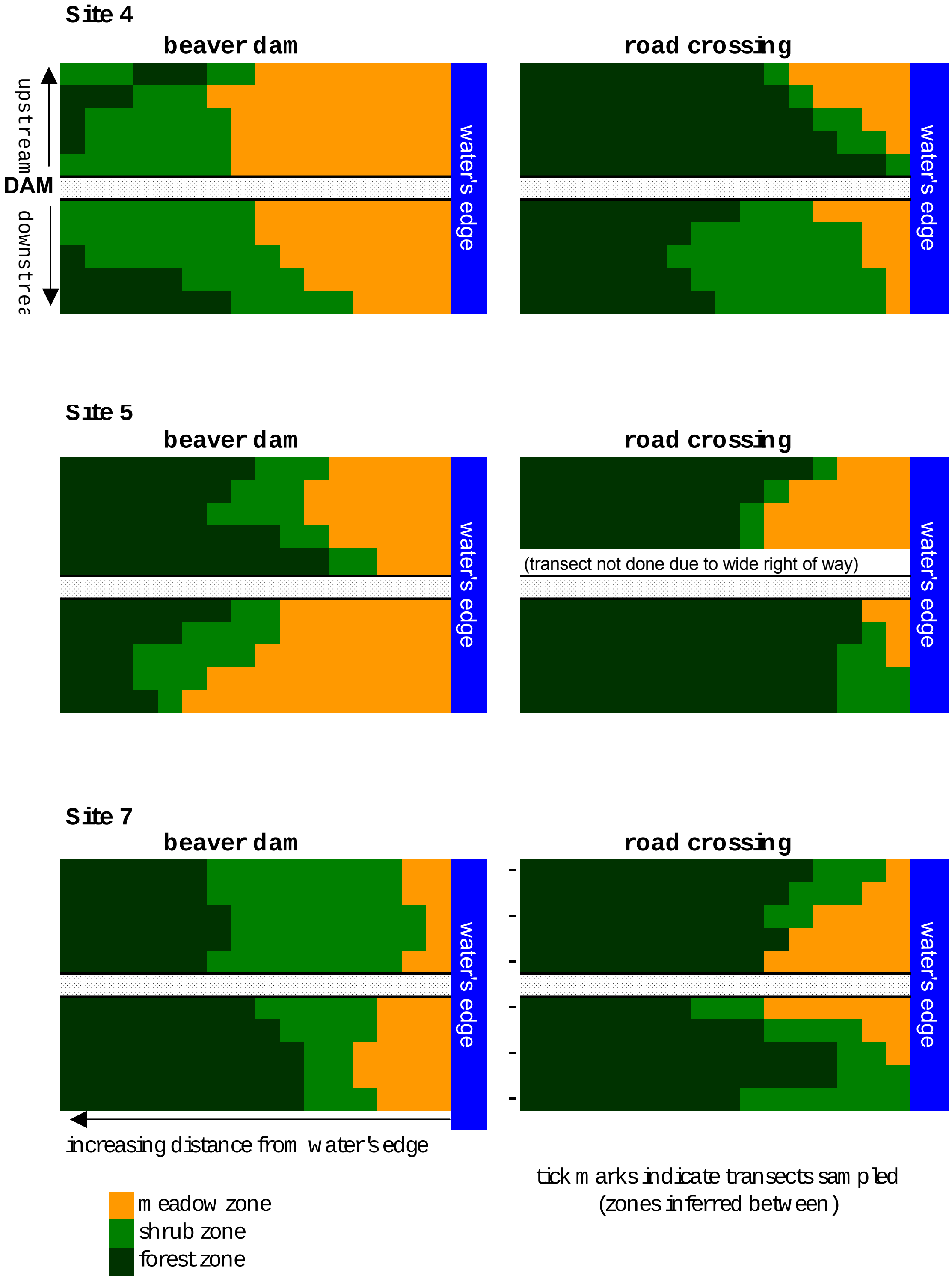
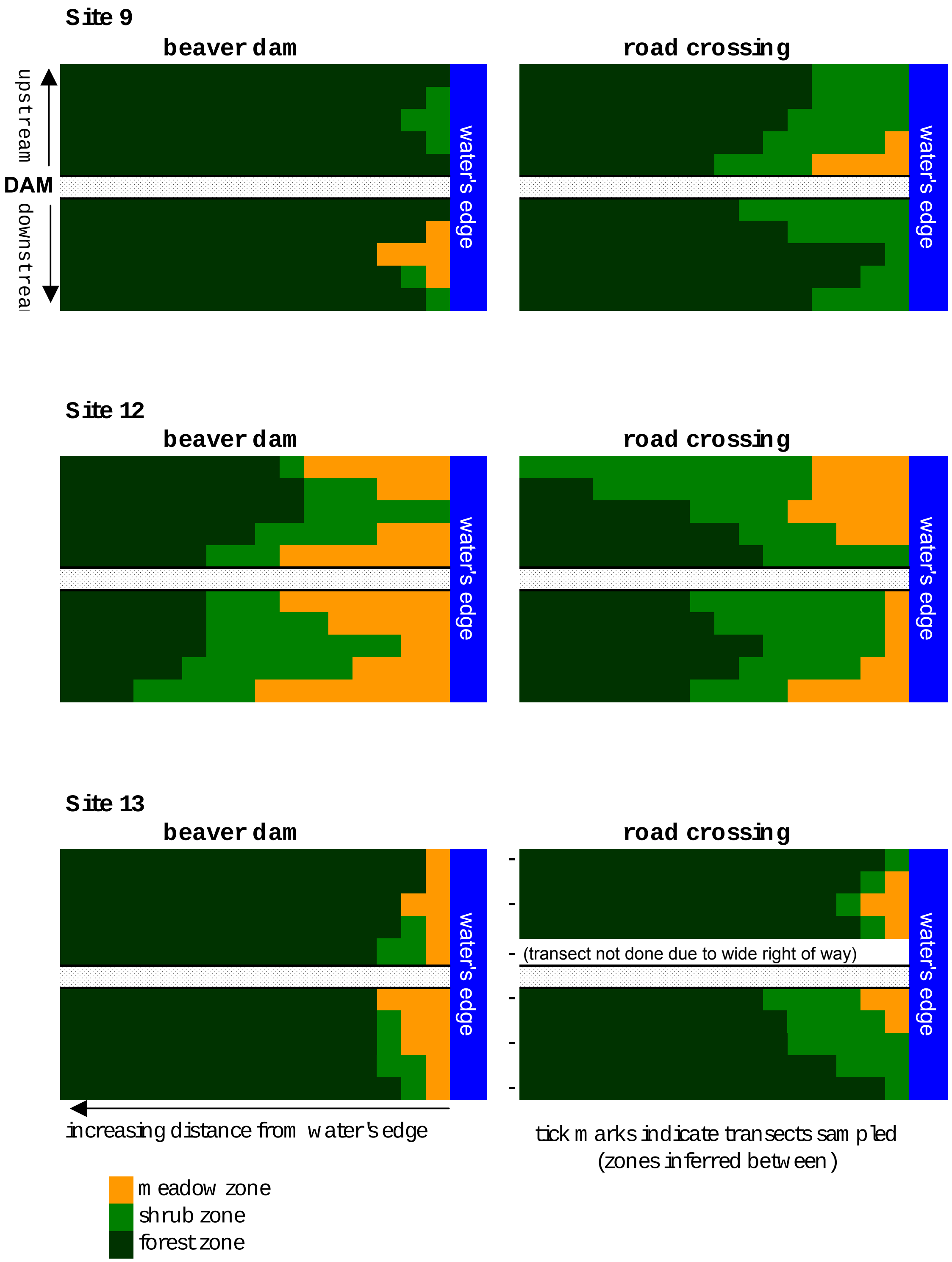


Figure A4.4 (cont'd) Visual representation of vegetation zones at road crossing and beaver dam at each site.



Appendix 4 b. Sapling Density at Road Crossings and Beaver Dams

I used Wilcoxon signed-ranks tests to compare overall density and relative proportion of deciduous saplings at dams and road crossings. Per treatment densities were calculated using a total count per treatment at each site, i.e. pooling across transects. I used a 2-factor split-plot ANOVA to test for differences in per treatment proportion of deciduous saplings at road crossings compared to beaver dams. For these analyses, the factors tested were wetland type (beaver or road; fixed factor) and treatment (up- or downstream; fixed factor), blocking by site (random factor). The model was the same as for zone widths (above) except that the dependent variables Y_{ijk} = deciduous sapling density. I used the per treatment proportion deciduous saplings, rank transformed, and a generalised linear model (GLM) test procedure in the comparisons.

Deciduous sapling density was not significantly different between beaver dams and road crossings (p=0.917, Figure A4.5). The proportion of deciduous saplings was higher at the road crossing at 4 out of 6 sites (Table A4.6) but this difference was not significant (p=0.173). The relative proportion of deciduous saplings per treatment appears to be different at road crossings and beaver dams. There was no statistical difference in the relative per treatment proportions of deciduous saplings between beaver dams and roads (p=0.127, Table A4.7), however, the overall proportion of deciduous saplings differed significantly among sites (p=0.002) and between beaver dams and roads (p=0.049; higher at roads).

Figure A4.5 Deciduous sapling density (count / 100m²) per wetland type at each site, pooled across treatments

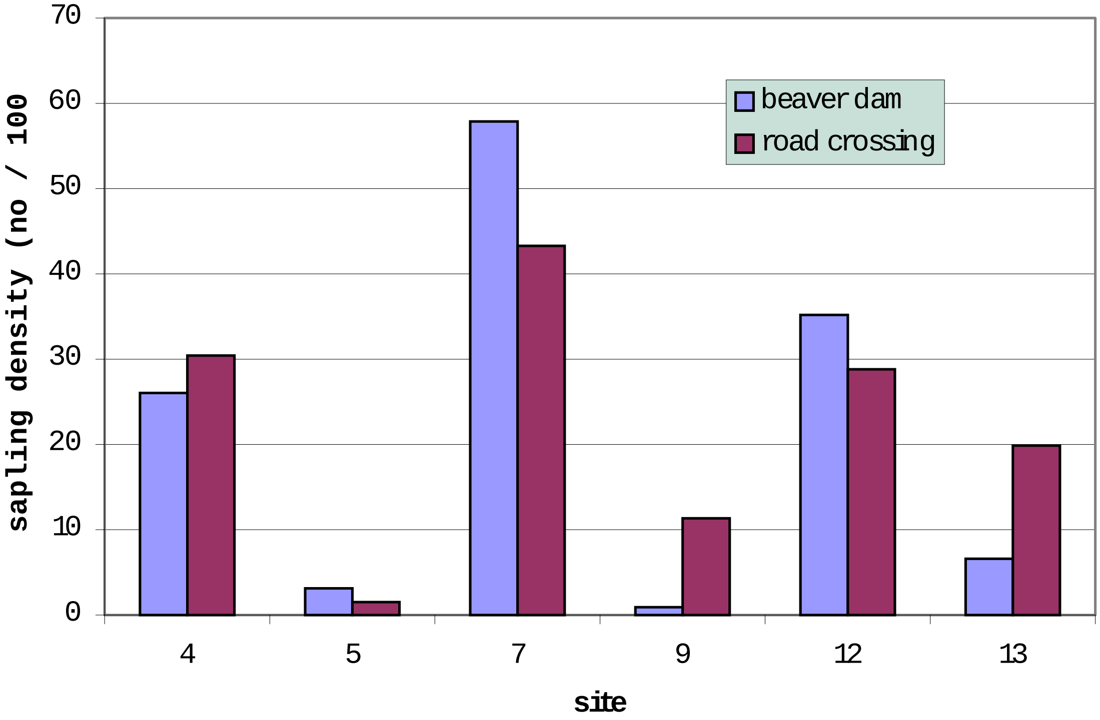


Table A4.6 Proportion of deciduous saplings (no. deciduous / no. all species) per wetland type at each site, pooling transects

Site	BEAVER DAM			ROAD CROSSING		
	up	down	total	up	down	total
4	0.25	1.00	0.85	0.99	1.00	1.00
5	0.38	0.57	0.45	0.58	0.08	0.30
7	1.00	1.00	1.00	1.00	1.00	1.00
9	0.13	0.00	0.07	0.41	0.05	0.20
12	0.56	0.87	0.76	0.96	0.96	0.96
13	0.50	0.24	0.39	0.69	0.52	0.61
Average	0.47	0.61	0.59	0.77	0.60	0.68

Type is road crossing or beaver dam within each site.

Treatment is upstream or downstream of road crossing or beaver dam.

Table A4.7 Results of split-plot ANOVA test for effects of site, wetland type, and treatment on proportion deciduous saplings

Source	df	SS	MS	Fobs	p
site	5	806	161.2	22.493	*0.002*
type*	1	48.167	48.167	6.721	*0.049*
treatment~	1	1.5	1.5	0.077	0.787
treatment x type	1	54	54	2.776	0.127
site error	5	35.833	7.167		
error	1	194.5	19.45		
total	10	1140			

* beaver dam or road crossing
~ upstream or downstream

Proportion deciduous saplings was calculated as (number deciduous saplings / total number of saplings), pooled across transects within each treatment.

Table A5.1 Canopy basal area in forest zone for *Populus*, conifers, and all species combined at each site

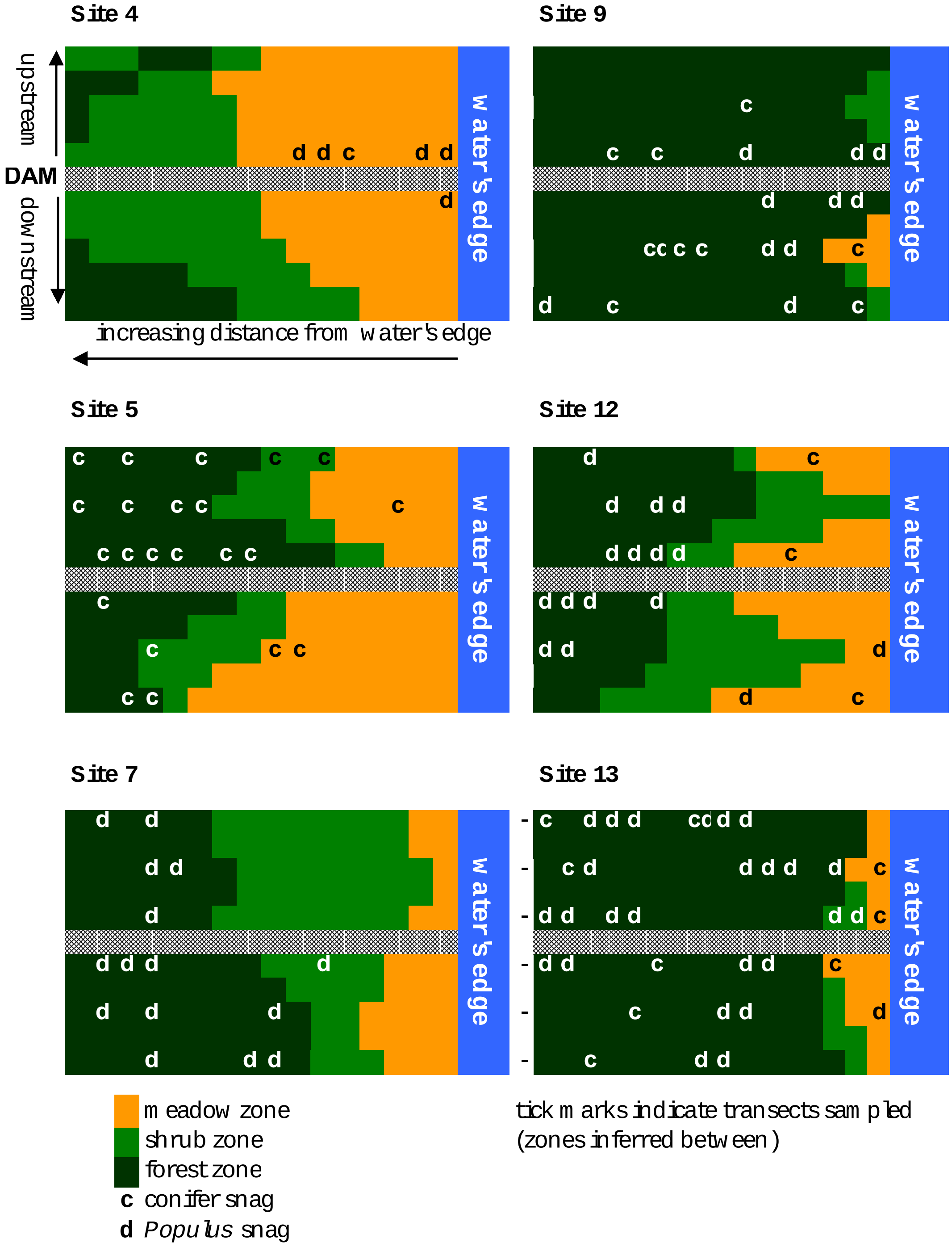
Site	total basal area (m 2/ha)			basal area (m 2/ha) per unit forest		
	Populus	conifer	total	populus	conifer	total
4	244.131	0	244.131	20.393	0	20.393
5	0.000	1849.821	1849.821	0.000	47.417	47.417
7	2175.875	9.831	2185.706	46.292	0.198	46.490
9	360.461	2755.890	3116.351	3.998	30.618	34.615
12	1735.129	370.292	2105.421	43.368	9.261	52.629
13	498.092	3511.220	4009.312	6.072	42.828	48.899

*basal area per unit forest was calculated as basal area / number of plots in forest zone

Table A5.2 Snag abundance upstream and downstream at each site, for *Populus*, conifers, and all species combined

Site	Populus		conifer		all species	
	up	down	up	down	up	down
4	6	2	1	0	8	2
5	0	0	23	9	23	9
7	5	11	0	0	6	14
9	3	8	3	7	8	16
12	9	10	3	1	13	11
13	20	12	8	5	29	17
Average	7.2	7.2	6.3	3.7	14.5	11.5

Figure A5.1 Snag presence in vegetation zones at beaver dams (presence of at least one dam in plot)



tick marks indicate transects sampled (zones inferred between)

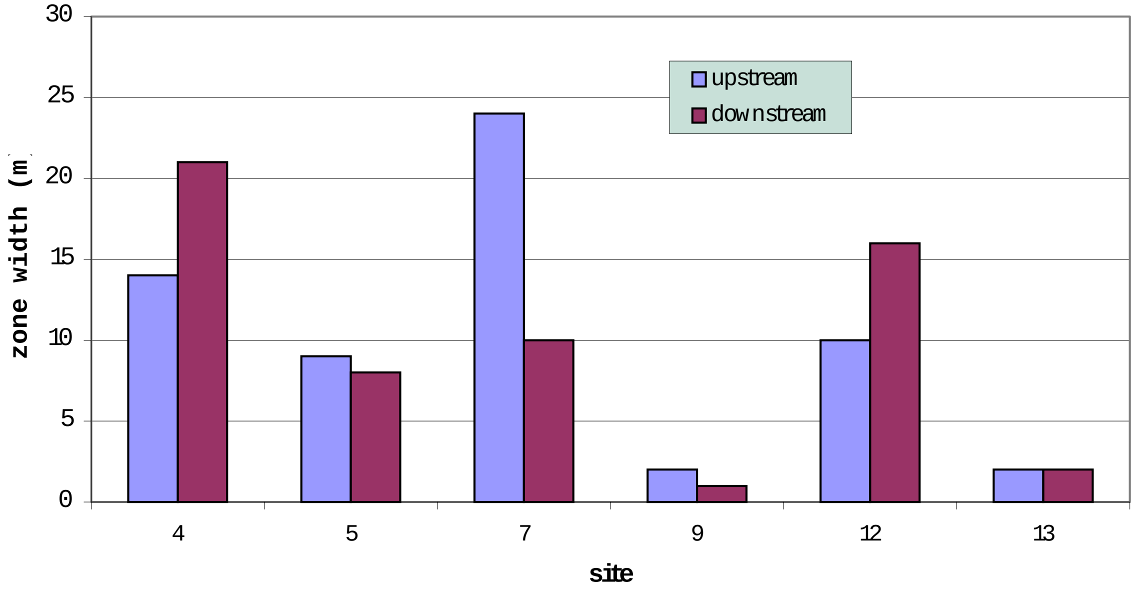
Table A5.3 Average vegetation zone widths (m)^ per treatment at each site

Site	meadow		shrub		forest		nonforest	
	up	down	up	down	up	down	up	down
4	30	19	14	21	4	8	44	40
5	14	26	9	8	25	14	23	34
7	5	10	24	10	19	28	29	20
9*	0	3	2	1	46	44	2	4
12	13	17	10	16	25	15	23	33
13*	4	6	2	2	42	40	6	8
Average	11	14	10	10	27	25	21	23

* new site

^ data converted from no. of plots to approximate distances, for interpretability

Figure A5.3 Average shrub zone width (m) per treatment at each site. Data from each site are shown to highlight variability.



Width represents distance from downslope edge to upland edge of each vegetation zone, averaged across transects within each treatment at each site. Plots were “zoned” using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

Table A5.4 Contingency table analyses of number of plots in each vegetation zone per treatment, pooled across sites

treatment	meadow	shrub	forest	Total
upstream	66 (74)	61 (60)	161 (155)	*288*
downstream	81 (74)	58 (60)	149 (155)	*288*
Total	*147*	*119*	*310*	***576***

X2 = 2.07

X2 crit (0.05, df=2) = 5.991

Plots were "zoned" using a subjective assessment of stem density and relative % cover of trees, shrubs, and grasses / sedges.

Figure A5.4 ***Populus*** **and** ***Salix*** **stump presence in vegetation zones at beaver dams**

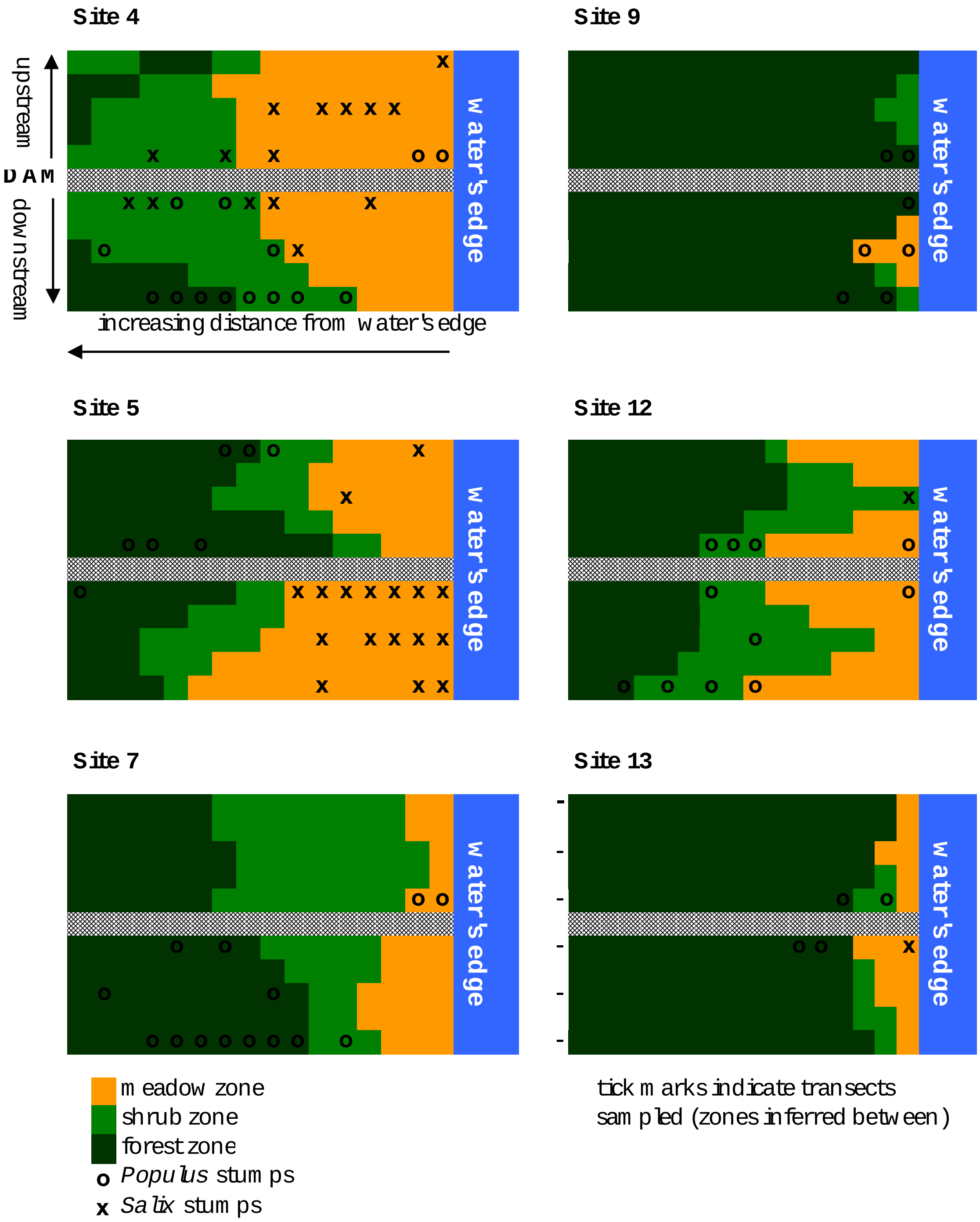


Figure A5.5 Relationship between stump diameter and distance from water's edge at each site, pooled across treatments

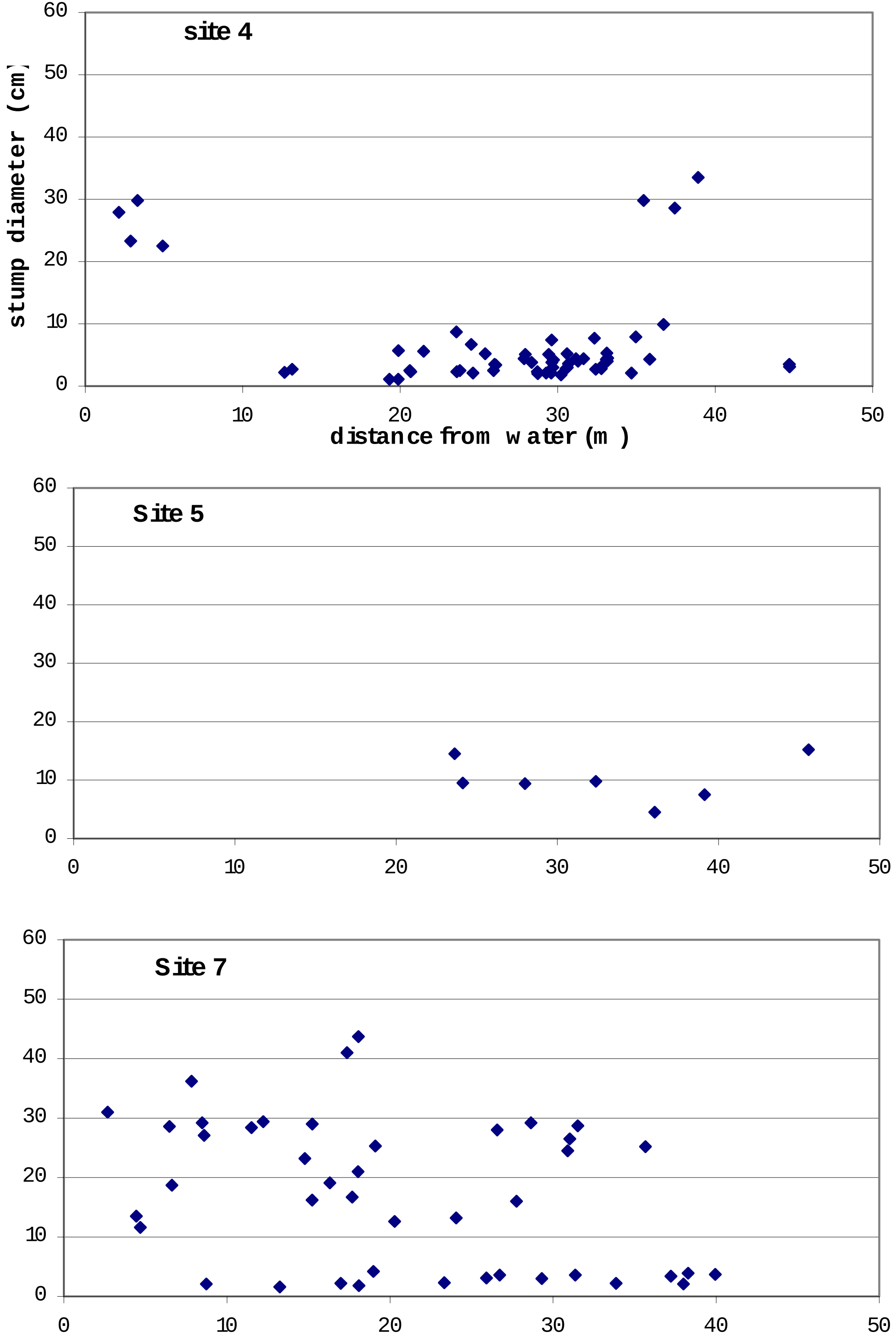
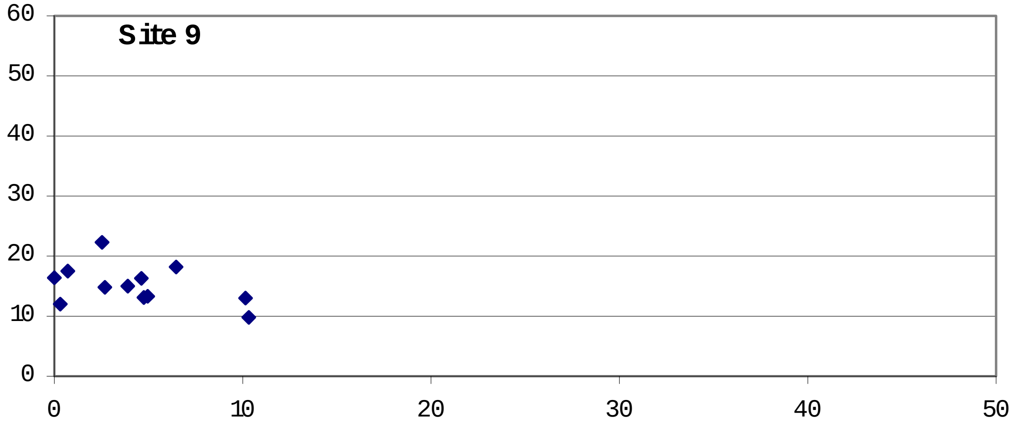
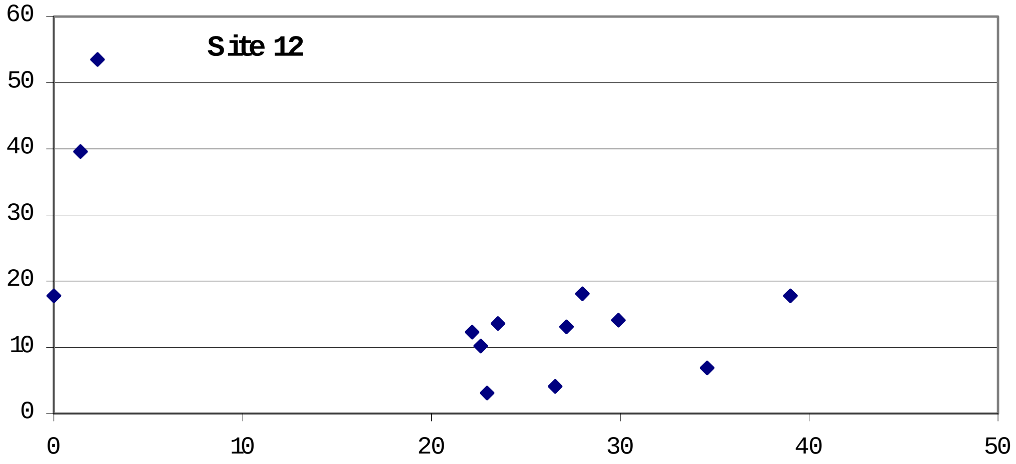


Figure A5.5 Relationship between stump diameter and distance from water's edge for each site, pooling across treatments (cont'd)





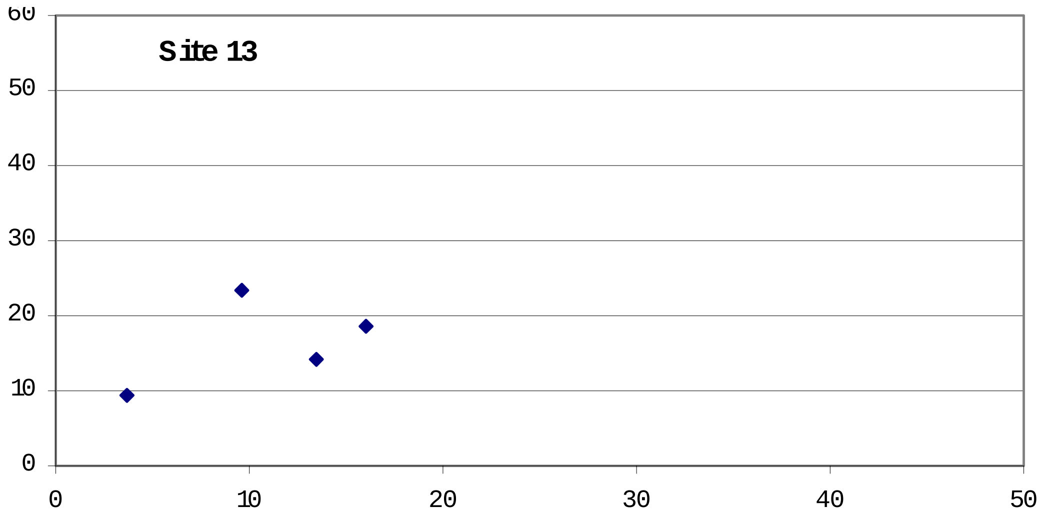
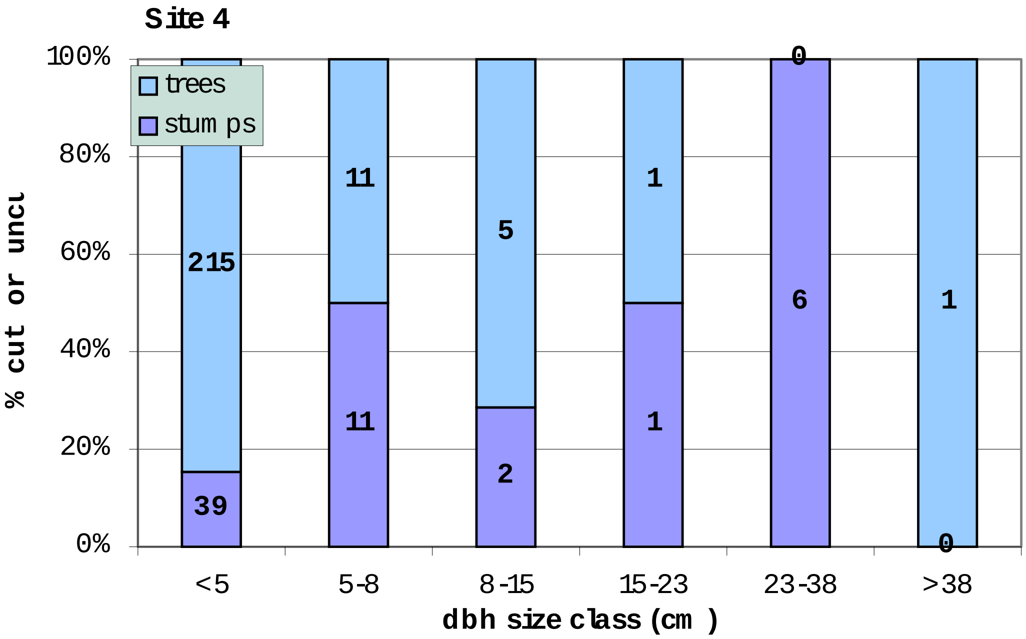


Figure A5.6 Proportion of *Populus* trees cut in each size class at each site, pooled across treatments

(count printed in each column)



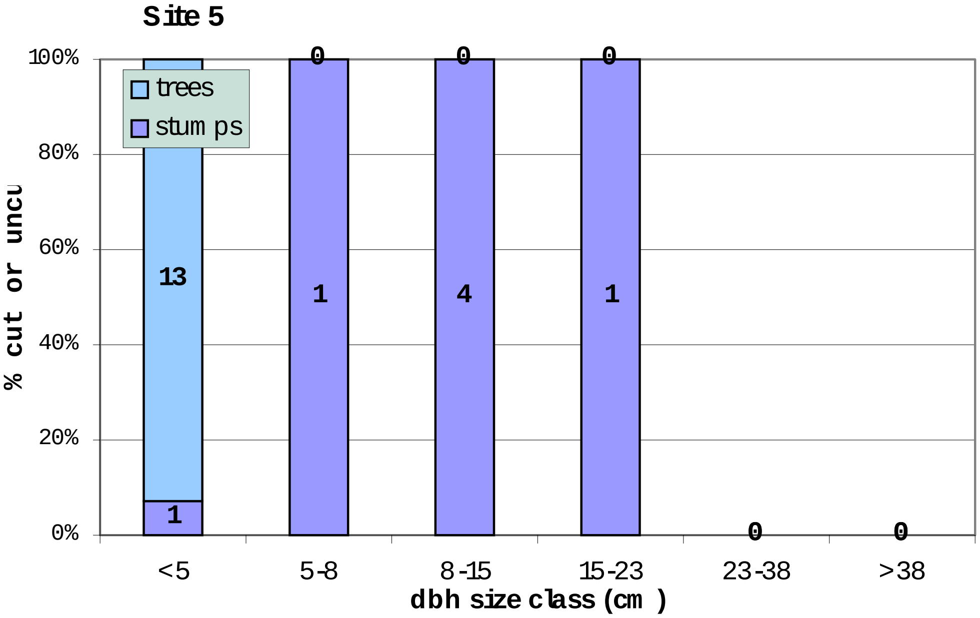
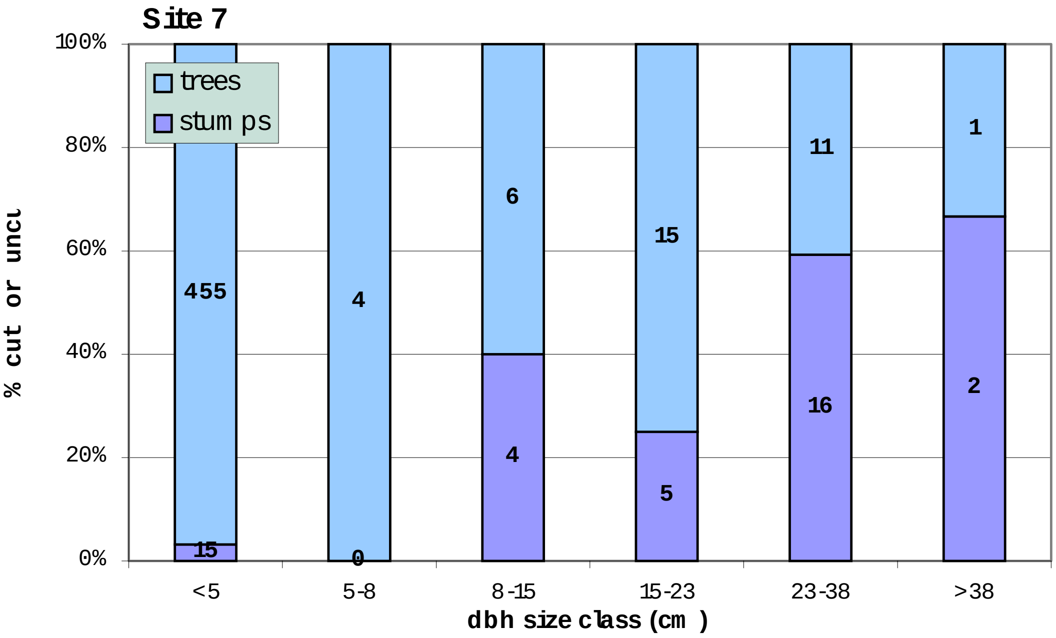


Figure 4.13 Proportion of *Populus* trees cut in each size class at each site, pooled across treatments (cont'd)

(count printed in each column)



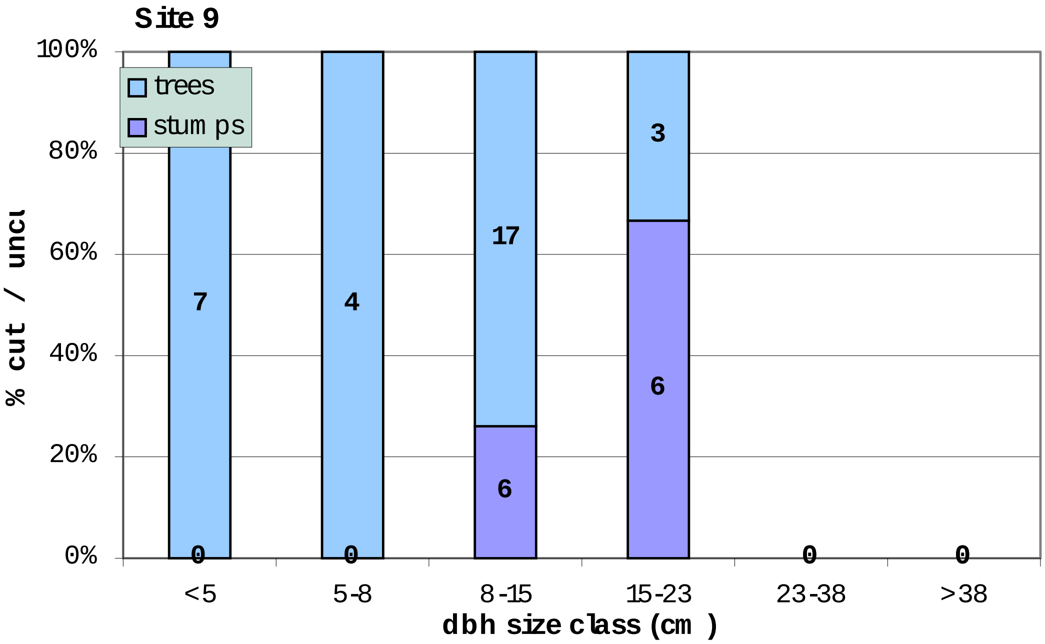
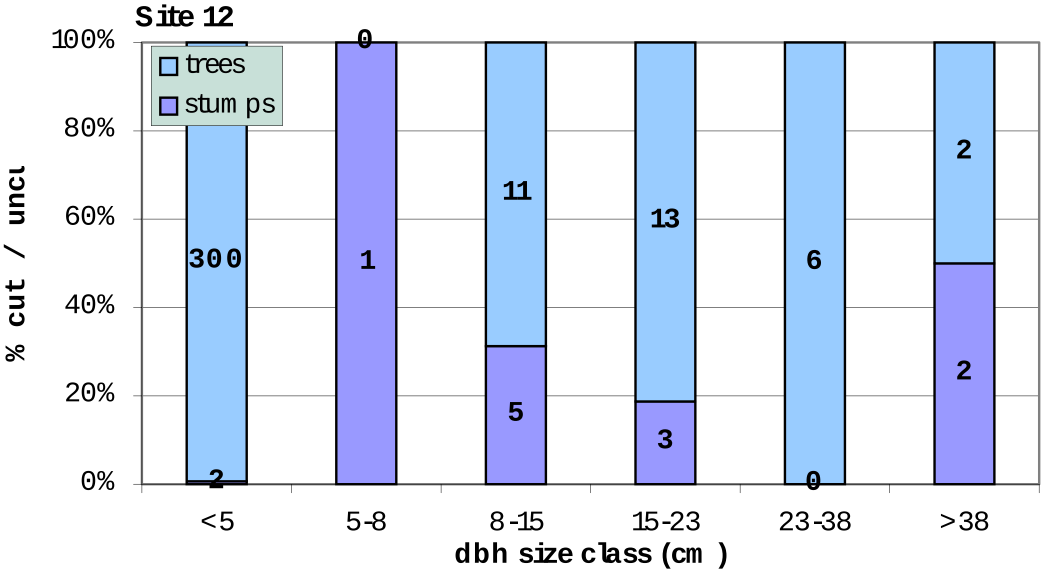


Figure 4.13 Proportion of *Populus* trees cut in each size class at each site, pooled across treatments (cont'd)

(count printed in each column)



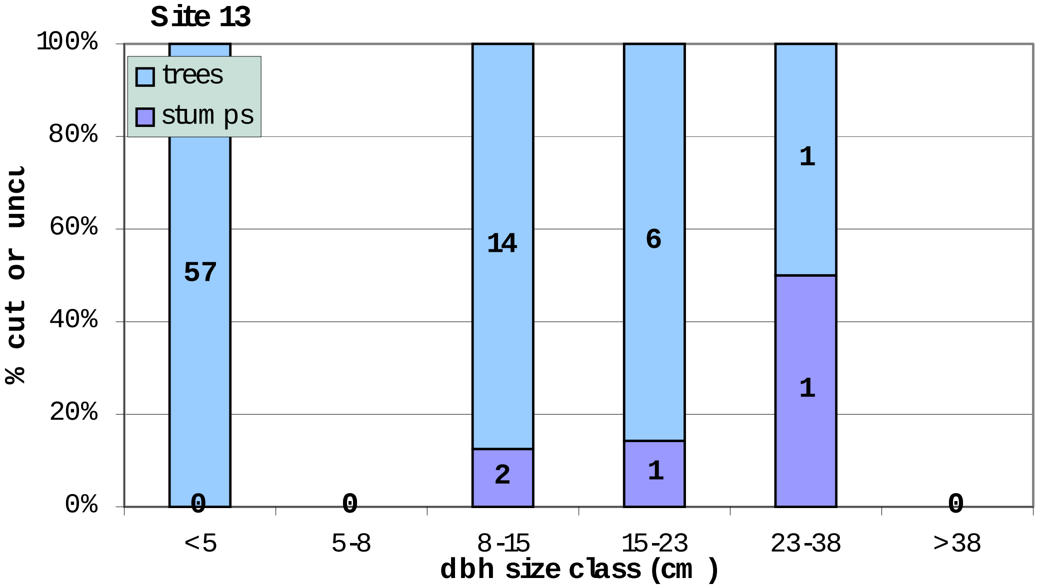
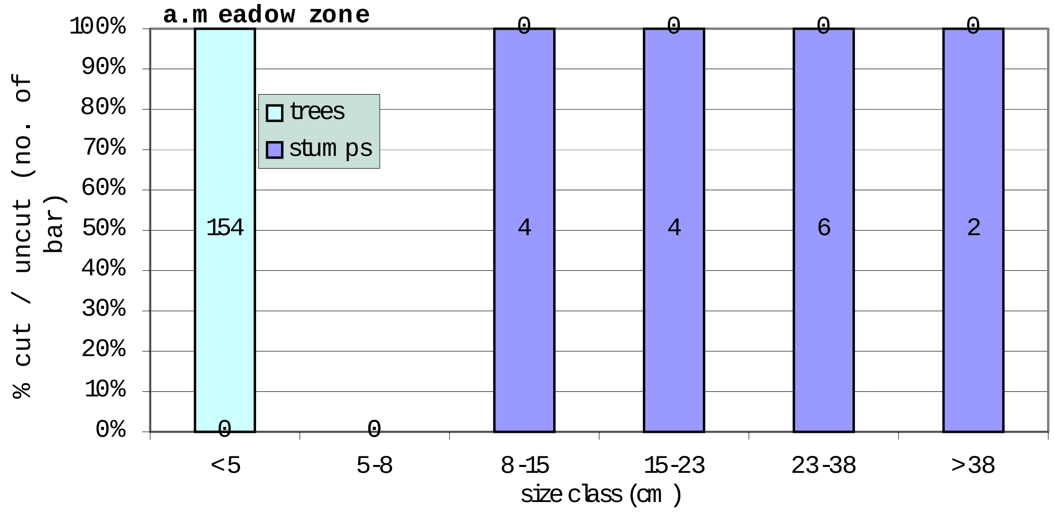
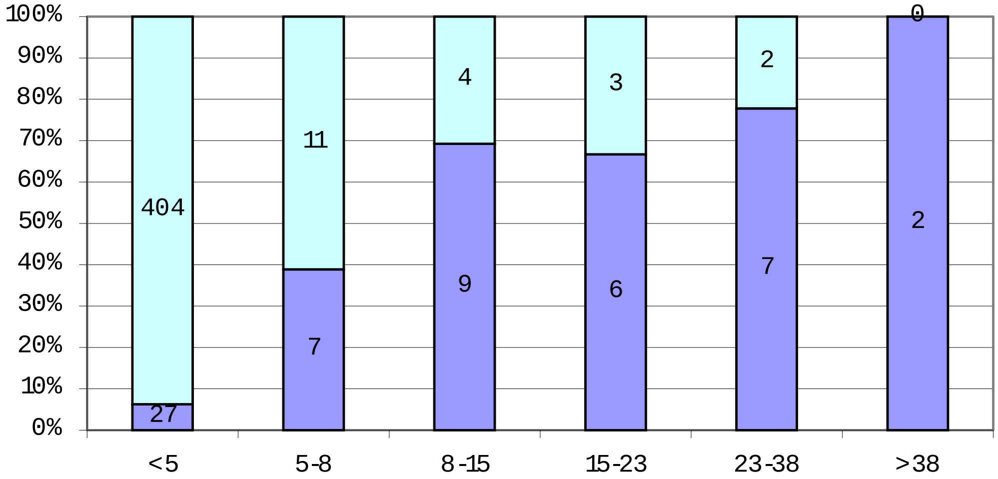


Figure A5.7 Proportion of *Populus* trees cut in each size class in each vegetation zone, pooled across treatments and sites


a. meadow zone


b) shrub zone

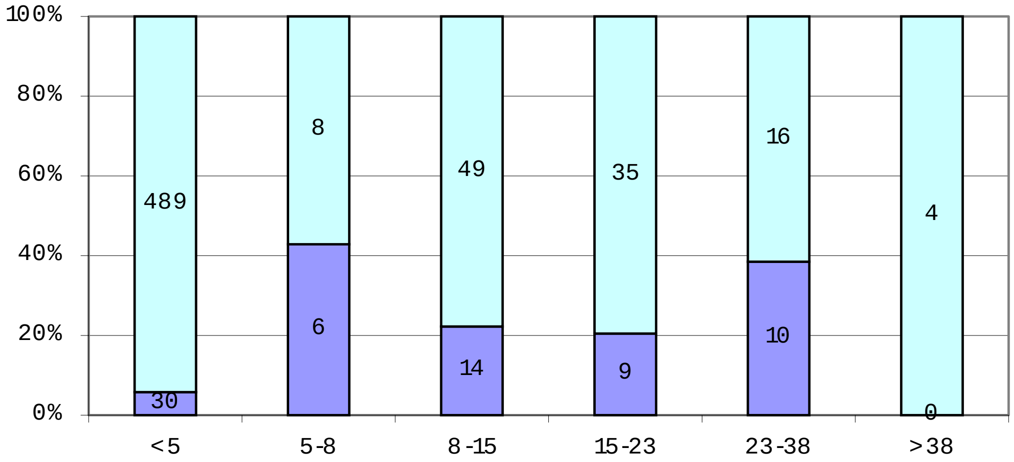

c) forest zone

Table A5.5 Number of saplings per unit forest and per unit basal area for *Populus* and conifer, at each site, pooled across treatments

Site	**no. saplings in forest**		**no. saplings / unit forest***		**no. saplings / unit basal area^**	
	Populus	conifer	*Populus*	conifer	*Populus*	conifer
4	75	15	6.25	1.25	502.1	--**
5	2	14	0.05	0.36	--**	12.40
7	300	0	6.38	0	225.9	0
9	7	112	0.08	1.24	31.9	66.59
12	51	73	1.28	1.83	48.2	322.88
13	54	87	0.66	1.06	177.7	40.59

* calculated as (total number of saplings in forest zone) / (number of plots in forest zone)

^ calculated as (total number of saplings in forest zone) / (basal area of species in forest zone)

** no trees > 5 cm dbh present

Figure A5.8 Average number of *Populus* saplings (<5 cm dbh) with distance from water's edge, pooled across treatments

(data are average sapling abundance per plot)

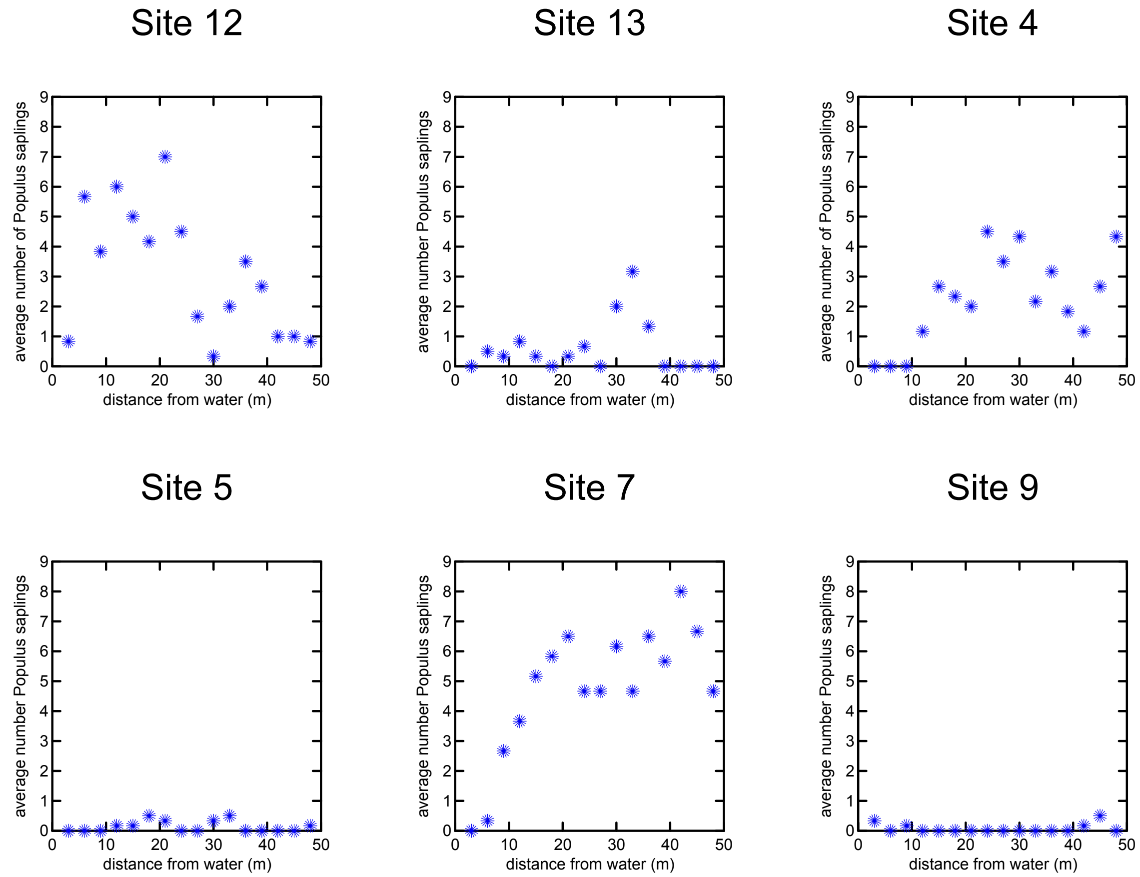


Figure A5.9 Average number of conifer saplings (<5 cm dbh) with distance from water's edge, pooled across treatments

(data are average sapling abundance per plot)