

**Spatio-temporal dynamics of the vegetation and seed bank of beaver
meadows in Riding Mountain National Park, Manitoba**

By

Michael P. Shaw

A thesis presented to the University of Manitoba in partial fulfillment of the requirements
for a degree of Master of Science in the Faculty of Graduate Studies

Department of Botany
University of Manitoba
Winnipeg, Manitoba R3T 2N2

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SPATIO-TEMPORAL DYNAMICS OF THE VEGETATION AND SEED BANK OF BEAVER
MEADOWS IN RIDING MOUNTAIN NATIONAL PARK, MANITOBA

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MASTER OF SCIENCE

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Abstract

The seed banks of beaver ponds and meadows, and the vegetation of beaver meadows, were examined along the upper reaches of the Little Saskatchewan River in Riding Mountain National Park, Manitoba. A total of eleven beaver meadows (one 1 year old, four 6 year old, four 9 year old, a 21 year old and a 22 year old), and six beaver ponds, were examined. The soils of the 11 beaver meadows were also examined for differences in five soil factors: soil moisture, pH, organic matter, bulk density, and conductivity. The vegetation and soil data were examined using canonical correspondence analysis. The results indicated that the vegetation of beaver meadows does change with age and soil factors. The youngest meadows are characterized by high cover of annuals and short-lived perennial plant species. By the sixth year, the grass *Calamagrostis canadensis* and the sedge *Carex atherodes* come to dominate all sites. The oldest meadows are drier have the highest shrub densities. The seed banks of beaver meadows are dominated by annual and short-lived perennial plant species, and become less and less similar to the extant vegetation with increasing meadow age. The composition of the seed bank of full beaver ponds was significantly different from that of beaver meadows, and showed lower species richness. There is some evidence that the seed bank of each pond is somewhat unique, with a floristic trend from the most upstream to the most downstream sites. The pond seed banks were most similar to the vegetation of the one-year-old meadow.

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Chapter 1 Introduction and Literature Review

1.1 Description Of Manitoba Escarpment and Area

Introduction

Riding Mountain is a 297,615 ha National Park located on the Manitoba Escarpment in the province of Manitoba, Canada (Fig 1.1). The Manitoba Escarpment and its associated highlands run in a north-west to south-east direction, from the Porcupine Hills (52°50'N, 102°W to Turtle Mountain (49°N, 100°W) (Fig 1.2). This study focuses on the upper portions of the Little Saskatchewan River (Fig. 1.3), which is home to a large and healthy population of beaver (*Castor canadensis* Kuhl). This population has had a significant impact on the wetland and forest vegetation along the rivers and its associated lakes and tributaries.

Geography

The Manitoba Escarpment occurs along the eastern edge of the Saskatchewan Plain physiographic region (Geological Survey of Canada 1987). To the east and below the escarpment lies the Manitoba plains physiographic region, which consists of sedimentary deposits from glacial Lake Aggasiz. The upper portion of the Little Saskatchewan River flows through the Moon Lake Ecological Land system (RMNP 1978).

The Moon Lake Ecological Land system is composed of Riding Mountain formation bedrock, with second-order topography provided by glacial deposits from the Wisconsin glaciation (Geological Survey of Canada 1987). The topography of the area is hummocky to undulating stagnation moraine. The area has low relief, with elevations ranging from 570

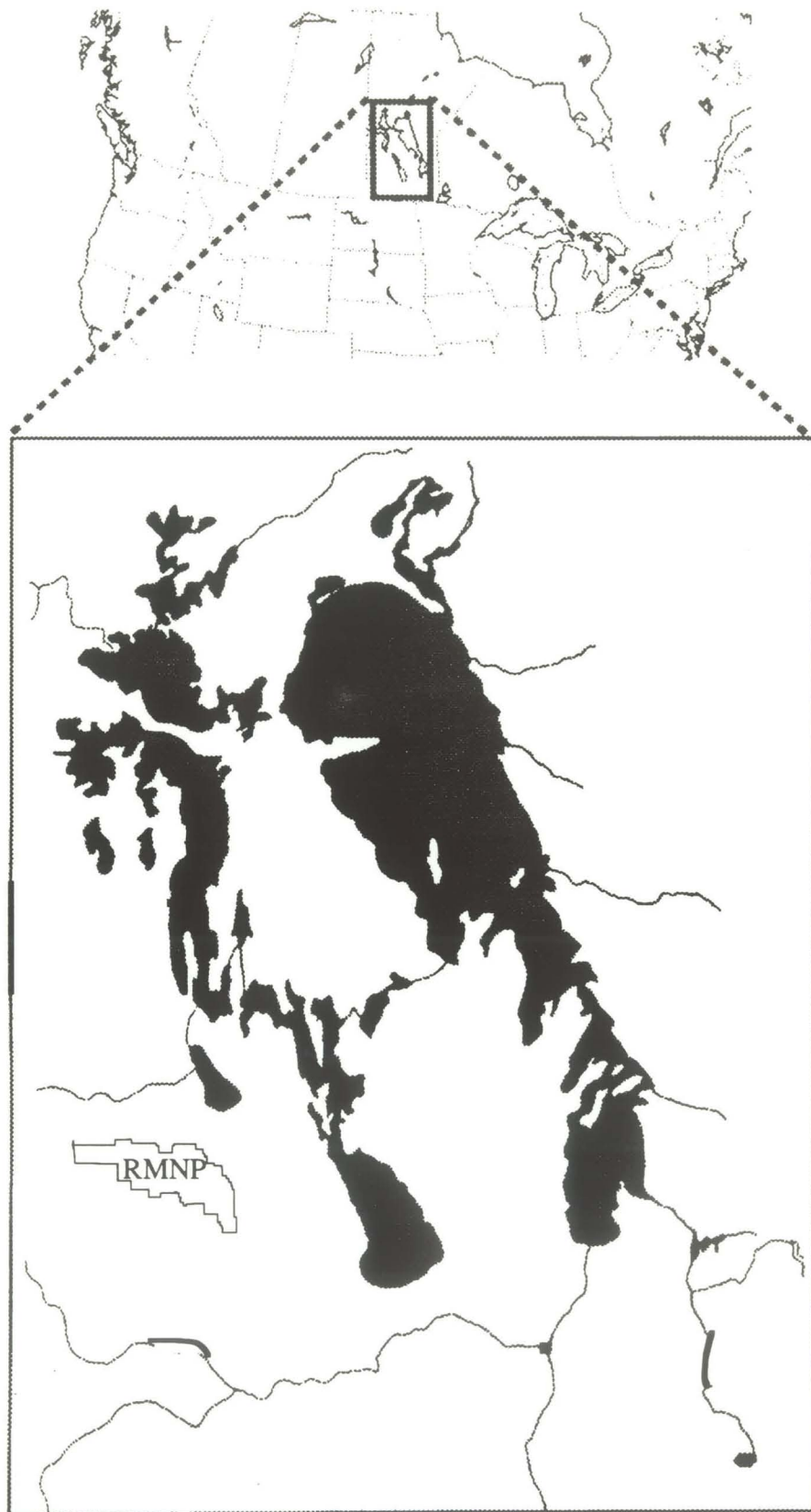


Figure 1.1 Manitoba in relation to North America.
The study was conducted in Riding Mountain National Park (RMNP).



Figure 1.2 Location of the Manitoba Escarpment. Dark Lines in the Southwest are the main faces of the Manitoba Escarpment. From the south to north: (1) Pembina hills; (2) Riding Mountain; (3) Duck Mountains and (4) Porcupine hills (1cm = 60km).

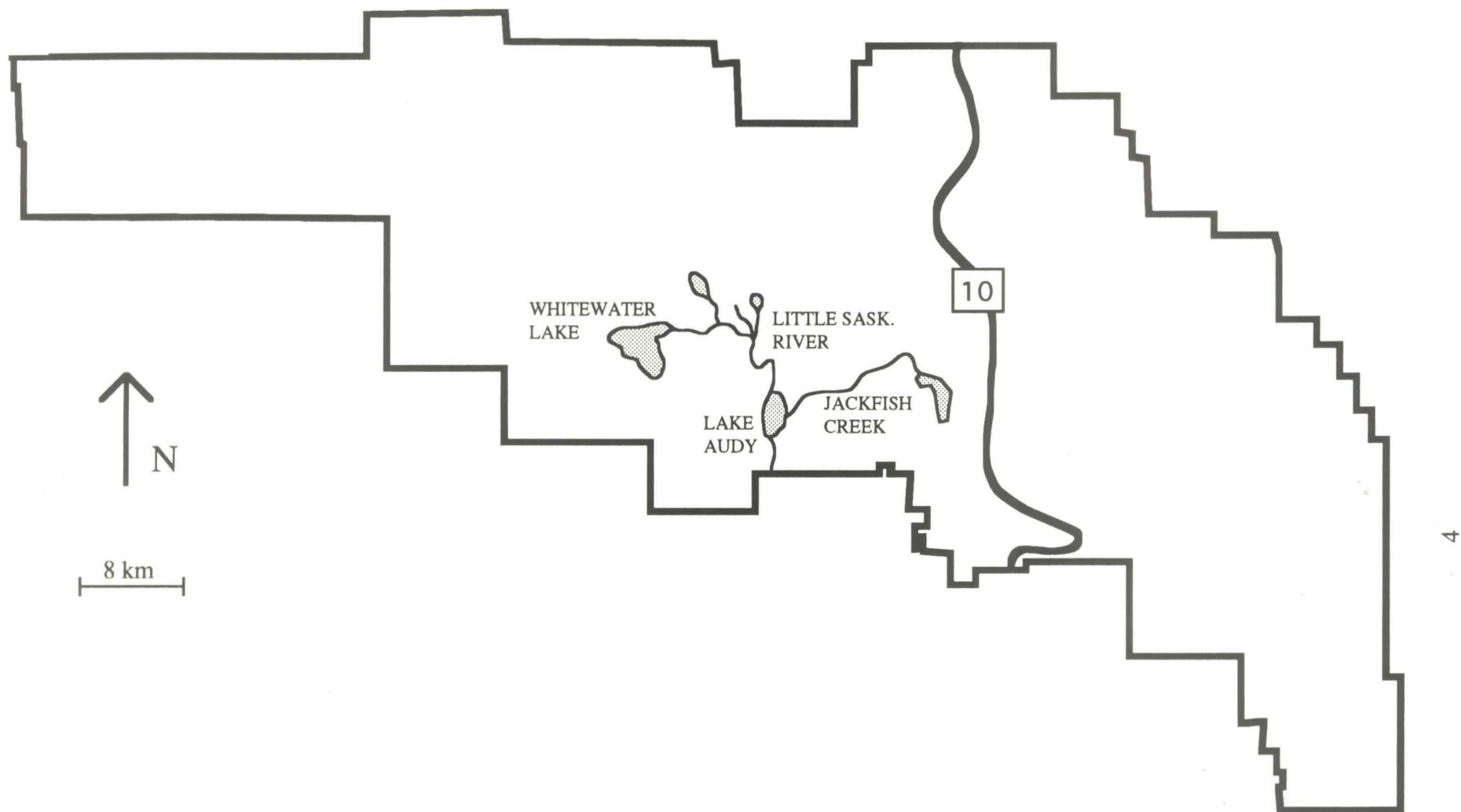


Figure 1.3 Riding Mountain National Park.
Beaver meadows were examined along the waterways shown.

m in the south-west to 720 m in the north-east. The Moon Lake highlands include the headwaters of the park's two major watersheds, the Little Saskatchewan and Vermilion river systems. The Vermilion River drains to the north-west, eventually emptying into Dauphin Lake. The Little Saskatchewan River flows south-west, draining into the Assiniboine River near the city of Brandon. Both rivers are part of the Hudson Bay drainage system.

Geology

The highland areas of Riding Mountain National Park are underlain by Cretaceous Period shale (Geological Survey of Canada 1987). This bedrock type extends along the Manitoba Escarpment from approximately 52°45'N to the United States border. This deposit, which occupies most of the south-west corner of Manitoba, is approximately 250 km wide at the border and narrows to the north (Geological Survey of Canada 1987). This Cretaceous bedrock has been divided into six geological formations along a north-east to south-west gradient. These formations, moving from the north-east (oldest) to the south-west (youngest), are the Swan River, Ashville, Favel, Vermilion River, Riding Mountain and Boissevain formations (Geological Survey of Canada 1987). The Swan River formation is composed of quartzose sandstone, glauconitic sandstone and kaolinitic shale laid down during the late Jurassic and early Cretaceous periods. This, the oldest formation of the six, has a maximum thickness of approximately 75 m and extends as a narrow band (10 to 60 km in width) from the Manitoba-Saskatchewan border just south of The Pas to the United States border near Winkler. The Ashville formation lies over this formation and extends along the same line immediately to the west. It contains carbonaceous shale, 'Ashville sand' and silt with a maximum depth of approximately 115 m. Further west is the narrow (5-10 km width) Favel formation, which contains calcareous speckled shale,

minor limestone bentonite and low grade oil shale and has a maximum depth of 40 m. The Vermilion River formation is composed of three members, from bottom to top: (a) Morden member, composed of dark grey non-calcareous shale and local sand and silt; (b) Boyne member, composed of grey speckled calcareous shale, with areas that are slightly petroliferous; (c) Pembina member, composed of dark grey carbonaceous non-calcareous shale with some bentonite bands. The Vermilion River formation has a maximum depth of 155 m and extends from the north slope of the Porcupine Hills to the United States border near Morden. This formation is widest in areas where it has been exposed by the erosive actions of the Assiniboine, Valley and Swan Rivers.

The Riding Mountain formation is the largest of the six (up to 200 km wide) and also the deepest, attaining a maximum depth of 310 m. It covers most of the south-west corner of Manitoba, including the Porcupine Hills, the Duck Mountains and Riding Mountain. Like the Vermilion River formation it is composed of three members. These are, from bottom to top: (a) Millwood member; (b) Odanah member, which includes the present study area within Riding Mountain National Park; (c) Coulter member. All are characterized by non-calcareous Gray shale with ironstone and some bentonite bands near the base. Some natural gas deposits have been found within this formation.

The last is the Boissenvain Formation, which only occurs on the escarpment of Turtle Mountain. It is only 2-10 km in width and about 50 km in length around the Mountain. It has a maximum depth of 30 m and is composed of greenish gray sand and sandstone.

Soils

The geological parent materials of the upper escarpment of Riding Mountain include glacial till, glacio-fluvial or glacio-lacustrine deposits (RMNP 1978). Glacial till is the most

common of the three, and is the parent material within the Moon Lake Ecological Land System. The soils of the highland areas of Riding Mountain are derived from carbonate rock and therefore moderately to strongly calcareous in nature (RMNP 1978). The exception are the Tamarisk Lake, Bob Hill, Brule, and Birdstail Benchlands landform systems within the Park.

There are three soil orders present on highlands of the Riding Mountain Escarpment: the Luvisols, Gleysols, and Organics. The principal Great Soil Group is the Grey Luvisols (Weir 1983). This soil group, which is found in most of the forested uplands and in the grassland-forest transition zone (RMNP 1979), consists of imperfectly-drained mineral material. The soil has a light-coloured, leached A horizon and a clay-enriched B horizon. This soil group is generally neutral to slightly acidic in the upper levels, grading to calcareous alkaline material with increasing depth (Weir 1983).

The two other Great Soil Groups are found in small areas within the study region. Humic Gleysols are a minor wet soil component of the Riding Mountain highlands, and are found in hollows and level lowlands. They are characterized by a dark-coloured A horizon. Organic Mesisols are found along waterways of the Riding Mountain highlands. They are derived from partially decomposed herbaceous material, particularly grasses and sedges (RMNP 1979). The organic component of these soils is generally >30%.

Climate

According to the Koopen-Geiger Classification system the Riding Mountain highlands have a moist snowy-forest climate with cool, short summers and no discernible dry period (Strahler & Strahler 1987). The area has on average 105 frost-free days, from May 25-30 to September 10-15 (Weir 1983). Mean monthly temperatures range from -20.7°C in

January to 19.0°C in July, with a mean annual temperature of -0.3°C (Environment Canada 1981). Mean temperature during the frost-free period is 12.8° C. Mean annual precipitation is 546 mm, 353 mm (≈65%) of which falls as rain between May and September (Environment Canada 1981).

Vegetation

Riding Mountain lies within the Boreal Forest Region of Canada (Rowe 1972). Most upland areas of the Park lie within the Mixed Wood section of this forest region (RMNP 1979). Trembling aspen (*Populus tremuloides*) forest communities dominate many of the upland regions, though mixed trembling aspen-white spruce (*Picea glauca*) forests are also common. Together these two forest community-types cover approximately 84% of the Park (RMNP 1979).

In the forested wetland regions of the escarpment highlands black spruce (*Picea mariana*) and eastern larch or tamarack (*Larix laricina*) are commonly encountered. Non-forested wetland areas are of three types: (a) emergent macrophyte wetlands composed primarily of sedges and rushes (*Carex* and *Juncus* spp.); (b) wet graminoid meadows composed of grasses (mainly *Calamagrostis* spp.), sedges (*Carex* spp.) and shrub willows (*Salix* spp.); (c) shrub communities dominated by willow (*Salix* spp.), alder (*Alnus* spp.), sedges (*Carex* spp.) and horsetail (*Equisetum* spp.) (RMNP 1979).

Grassland communities are also sometimes found on the Riding Mountain highlands. Native rough fescue (*Festuca* spp.) prairie grasslands have been encroached upon by *Populus tremuloides* and *Salix* spp. in areas with fine-textured, moist soils. In areas of coarse-texture parent material, species such as shrubby cinquefoil (*Potentilla fruticosa*) and choke cherry (*Prunus virginiana*) are invading. Bluegrass (*Poa* spp.) and wheat grass

(*Agropyron* spp.) communities often establish in areas disturbed by logging and overgrazing (RMNP 1979).

1.2 Beaver effects on vegetation structure and composition

Introduction

The beaver (*Castor canadensis*) is the only species in North America that modifies stream channels by constructing dams. The species also affects the surrounding vegetation by the browsing and/or felling of trees and shrubs. This environmental impact can be considered a disturbance *sensu* Sousa (1984): “a discrete, punctuated killing, displacement, or damaging of one or more individuals or colonies that directly or indirectly creates an opportunity for new individuals (or colonies) to become established”. Dam construction by beavers is a disturbance, since the resultant flooding kills terrestrial species which in turn permits invasion by aquatic vegetation. Periodic draining and dam breaching reverses this trend, with the drained area again being colonized by terrestrial vegetation. Such disturbances also result in the alteration of the physiography and ecology of streams (Neff 1957; Naiman et al. 1988; Johnston & Naiman 1990a).

Beaver Family Structure

Beaver are normally found in colonies of three to eight (mean of five) individuals occupying a pond or stretch of river (Payne 1981; Dieter & McCabe 1989; Bergerud & Miller 1977). The colony utilizes a common food supply and maintains a common dam system and lodge (Bradt 1938; Howard & Larson 1985). The dam system along a stream is generally built such that a given pond backs onto the front of the next dam upstream

(Naiman et al. 1988). Regardless of the number of ponds maintained by a colony, there is usually only a single lodge.

The construction materials employed in building dams and lodges consists of logs, mud, rocks and twigs. To acquire logs, beavers actively cut down nearby trees and remove their branches. Larger branches are used in dam construction, while smaller ones become part of the food cache. Beaver will also burrow out deep channels in the ponds to facilitate the transportation of larger logs (Naiman et al. 1988).

There are thought to be a number of benefits associated with dam construction by beaver. In particular, the resultant increase in water surface area affords the species greater accessibility to terrestrial food supplies without being exposed to predators (Fair 1978). The building of dams also ensures that ponds remain relatively deep even during periods of drought. This is particularly important in the winter; the deeper the water, the less likely the pond is to freeze completely. Open water allows the beaver to reach its food cache without having to go aboveground.

Beaver Habitat Requirements

(a) Physical Requirements

Beaver habitat requirements include satisfactory physical and biological conditions (Howard & Larson 1985; McComb et al. 1990; Beier & Barrett 1987; Broschart et al. 1989; Chabreck 1958; Neff 1957; Gill 1972; Dieter & McCabe 1989). In general, the physical requirements reflect the ease with which dams can be constructed and maintained. Howard & Larson (1985) found that a number of hydrological conditions, including stream width, landscape gradient and soil drainage class, were important in habitat selection by

beaver. In their study area (Prescott Peninsula, Mass.), beaver populations showed a distinct preference for wide, slow-moving streams flowing through poorly-drained areas. McComb et al. (1990), working in Oregon, found that beaver preferred shallow streams and low landscape gradients. Based on these results, they suggested that while a minimum flow rate is required to make dam construction advantageous, beaver avoid high stream gradients since in such areas spring freshets will wash out their dams. They also suggested that shallow stream valleys are preferred since beaver can construct the lowest dams possible while flooding a large area. This contradicts a study in the Truckee River Basin, California (Beier & Barrett 1987), where a definite preference by beaver for the deepest parts of the streams was found. The authors argued that deeper stream channels possess greater underwater area, and thus more sites for food storage and a more reliable water supply during drought periods and over the winter months.

It could be argued that these contradictory results simply reflect the correlation found between stream depth and width by Beier and Barrett (1987), versus the correlation between stream gradient and depth found by McComb et al. (1990) and Howard & Larson (1985). Specifically, both stream gradient and stream width may be important in site selection, as they are both correlated with stream depth. Another possibility is that beaver populations in different physiographic and climatic regions employ different criteria in site selection.

The type of substrate may also be an important factor in site selection. McComb et al. (1990) found that beaver dams were only located in areas where the substrate was composed mostly of silt and soil. They suggested that beaver dams will not adhere adequately to rocky substrates. Another factor influencing beaver site selection is the size of the watershed (Howard & Larson 1985). These authors proposed that the larger the watershed above a given section of stream, the greater the likelihood that it will be utilized

by beavers. This may be true of smaller watercourses, but a negative relationship is expected for larger watercourses since beyond a certain river size (width and flow) it becomes impossible for beaver to construct or maintain the dam. McComb et al. (1990) suggest that the slope of the bank may be of secondary importance, since they found that the lower sloped banks had a greater number of associated beaver dams. However, bank slope was strongly correlated with other factors suggested as being important, including shallow depth and low gradient.

To summarize, two physical factors appear to be important in beaver site selection:

1. avoid sites that are susceptible to flooding of a magnitude that could destroy the dam, food cache, or lodge.
2. select sites that will not dry up during low water cycles, or completely freeze during the winter season.

Beaver may also construct bank lodges along larger water courses (e.g., Red River) and in slow-moving swampy areas (e.g., in boreal wetlands with little topography). Bank lodges may be more common than has been previously recognized (W.O. Pruitt, pers. comm.). Dieter & McCabe (1989) examined the physical and biotic factors affecting beaver lodge site selection along prairie rivers. They found that bank slope was the most important physical factor. They also found that river depth at lodge sites was significantly greater than randomly located sites along these rivers. Presumably beaver select such sites to ensure that the water does not completely freeze during the winter. Lodges built on prairie rivers generally have two underwater entrances. A steep bank provides sufficient water depth to conceal more than one entrance while enabling the beavers to construct large chambers above the water level.

(b) Biological Requirements

The biological requirements of beaver are seemingly varied. Among the biotic factors affecting site selection, the amount of hardwood in the region surrounding a center of the beaver pond appears to be the most important (Howard & Larson 1985). Their study examined the fate of beaver dams in Prescott Peninsula, MA shortly after beaver reintroduction in the early 1950's. The species was initially found only in sites characterized by large amounts of hardwood. Individuals began occupying less favorable sites only after the better sites were completely occupied. However, these less suitable sites were usually quickly abandoned, presumably because they lacked ample hardwood supplies. Howard & Larson (1985) proposed that another important factor may be the availability of underwater herbaceous vegetation as feed during the winter months, and cited the need for further research regarding this feeding behavior of beaver. In a study of beaver sites in eastern Oregon, McComb et al. (1990) found that the most important biotic factors in site selection were the amount of hardwood and total forest canopy cover. In northern California, Beier & Barrett (1987) found a strong correlation between site occupation and the absence of white fir (*Abies concolor*). This result probably reflects the low abundance of aspen and other hardwoods in areas of high white fir density.

In prairie habitats, site selection for a bank lodge is dependent on the vegetation cover of the riverbank (Dieter & McCabe 1989). These authors found that riverbank areas adjacent to extant lodges had significantly more vegetation cover (at both 10 m and 15 m from the river edge) than random selected sites along the river. Cattle grazing activity near the lodge and foraging region was also found to be important (Dieter & McCabe 1989). They suggested that ungrazed areas are associated with dense willow thickets, numerous small trees and riverine plants that provide ample food supplies and/or construction materials.

Atypical dam and lodge construction behavior by beaver has been observed in the southeastern United States (Chabreck 1958). Beaver in these areas do not construct lodges, but instead made bank lodges by burrowing into a stream or river bank. As water does not freeze in the deep south, and streams generally do not dry up, beaver need not spend the energy to construct elaborate dams. Furthermore, this population does not fell trees but simply gnaws and eats the bark at the tree base. The author found that barking usually did not result in extensive damage to or death of trees. More curiously, the species most commonly exploited in this way was loblolly pine (*Pinus taeda*), which hitherto had not been reported as being utilized by beaver.

Along the delta of the Mackenzie River a series of events, initially involving changes in the physical environment, leads to the enhancement of the biotic environment for beaver (Gill 1972). The process involves river channel sedimentation to form sand bars that are colonized and stabilized by balsam poplar (*Populus balsamifera*). The adjacent riverbanks, which are characterized by water-filled depressions, are used as lodge sites by beaver to exploit the sand bar poplar stands. Beaver abandon the site when the poplar supply is depressed by foraging activities. Gill (1972) proposed a cyclical pattern of beaver exploitation of these poplar populations.

Resource Utilization

Ringelman (1991) found that four acres of mature aspens and an associated 12 acres of willows (*Salix spp.*) is necessary to support up to four beaver colonies.

Masslich et al. (1988) examined the dietary minerals available in four different beaver forage classes: (a) mature aspen twigs removed from felled trees; (b) mature aspen bark; (c)

aspen sapling twigs less than 5 cm in diameter; (d) aspen sapling bark. Calcium content of twigs from mature trees was greater than that of saplings. The authors observed beaver passing through areas of high aspen sapling density near their pond to cut down mature trees in more distant areas. When these trees were felled, the upper twigs were removed. Interestingly, the beaver utilized twigs that were the same size as those available from the more abundant saplings. They speculated that the need for some dietary mineral found in higher quantities in mature aspen twigs (quite possibly calcium) motivates such behavior. Another possibility is that the felling of large trees affords protection from large predators, since trees fall in such a way that it is difficult for large mammals to move about in the area.

Beaver are central-place foragers, since they move from a given point in search of resources and then return to that point with the resource. This behavior contrasts with the roving-forage method (in which the resource is consumed at the site of acquisition) associated with boreal forest herbivores such as moose, elk and deer. McGinley & Whitham (1985) found that beaver will selectively use food of higher nutritional value as the distance from pond to food source increases. This result complements observations of exploitation of aspen by beaver made by others (e.g., Hall 1957, Mitton & Grant 1980). Specifically, it was found that as a beaver travels to the limits of its foraging zone, it removes only easily-transportable branch sizes from the felled trees. Branch size is important since the time spent by the beaver at the site of the felled tree is limited. By contrast, when a tree is felled near a beaver pond, all branch sizes are removed since time is not limited in such cases (McGinley & Whitham 1985). This selective behaviour maximizes the food return given the higher risks of predation and other costs associated with more distant sites.

Once a beaver has brought a sufficient abundance of twigs to the pond a food raft is generally constructed (Fair 1978). Knowledge by beaver of energy availability is expressed

in the accurate placement of low food value items on the top of the raft, and highest food value items at the bottom. When the pond water freezes in winter the top portion of the food raft becomes encased in ice and thus unavailable to the beaver. However, the high food value items selectively placed at the bottom of the raft are available. Fair (1978) suggests that this use of low food valued items could explain the felling of conifer tree species (which have low food value) by foraging beaver.

As we have seen the aspen-beaver association is very strong. Hall (1957) proposed that the distribution of beaver in North America is largely determined by aspen availability. However, beaver will utilize other members of the Salicaceae (e.g., other species of the genus *Populus*, and *Salix* spp.) when trembling aspen is not available (McGinley & Whitham 1985; Hall 1957; Naiman et al. 1986; Mitton & Grant 1980). Hall (1957) found that the consumption rate of *Salix* spp. is inversely related to the amount of aspen present. Beaver have been observed to utilize conifer species when both trembling aspen and willows are absent (Beier & Barrett 1989). The unusual habit of barking of the lower trunk of white fir was observed by Hall (1957) in an area where trembling aspen was abundant. It was hypothesized that the bark might contain an unknown but required food compound.

Beaver distribution and density

Historical Patterns

The beaver has one of the broadest distributions of all North America mammals. The success of the species has been checked only by the vigorous trapping by early Europeans. The fur trade was in full swing by the early 17th century (Naiman et al. 1988), and by 1640 over 80,000 beaver were being trapped per year in western New York state alone (Hays 1871; Naiman et al. 1988). By 1673 between 50,000 and 200,000 beaver per year

were being removed annually from what is now Manitoba (Novak et al. 1987). Expeditions into the 'west' were largely motivated by the loss in revenues from dwindling beaver pelt supplies along the eastern seaboard (Cline 1974). Estimates of the western beaver population prior to trapping range from 40 to 400 hundred million over an area of some 15.5 million km² (Ringelman 1991; Naiman & Melillo 1984). This population was so severely exploited that by the end of the 19th century the species had been trapped to near extinction (Johnson & Chance 1974).

Evidence of beaver occupation has been found over most of the North American continent. The most northern occurrence of the species is along the MacKenzie River delta in the northern Yukon. A high population density (some 2000 colonies in the 6400 km² delta) occurs there (Gill 1972). The species occurs as far south as northern Mexico. Sighting in extreme southern locations are rare, however. Large populations are present in the some southern states, specifically Louisiana to California (Chabreck 1958; Beier & Barrett 1989).

Population Densities in Various Regions

The distribution of beaver over the continent is variable (Table 1.1), with published values ranging between 0.38 colonies/km² in the Truckee River basin (Beier & Barrett 1989) to 1.2 colonies/km² in Voyageurs National Park, Minnesota. In Canada, values of 0.76 colonies/km² (Algonquin Park, Ontario) and 0.51 colonies/km² (Newfoundland) have been reported.

Table 1.1 Range of beaver density that have been reported in North America

Author	Density (colonies/km ²)	Location
Howard & Larson (1985)	0.58	Prescott Peninsula, MA.
Bergerud & Miller (1977)	0.51	Newfoundland.
Voigt et al. (1976)	0.76	Algonquin Park, Ontario.
Beier & Barrett (1989)	0.38	Truckee River Basin, California.
McComb et al. (1990)	1.0	Long Creek Basin, Oregon.
Broshchart et al. (1989)	1.2	Voyageurs Nat. Park, MN.

Determination of Beaver Population Densities

Among the methods available to determine beaver population densities, aerial photography has proven the most useful (Payne 1981; Beier & Barrett 1989; Bergerud & Miller 1977; Johnston & Naiman 1990a; Howard & Larson 1985). Photographs are generally examined under 3X stereoscopic magnification to determine the number of intact beaver dams within the study area. In addition, the number of food caches (structures that beaver construct for winter feeding) associated with the dam can be determined. From these two values the number of beaver colonies in an area can be estimated (Johnston & Naiman 1990a; Howard & Larson 1985). Johnston & Naiman (1990c) have proposed that a raster-based geographic information system (GIS) using aerial photography be employed to both determine beaver density and to examine the effect of beaver on the surrounding vegetation. Aerial censuses from fixed wing or rotary aircraft have also been used (Payne 1981). Aerial censusing using helicopters is approximately 80% accurate, but only 60% accurate when small planes are employed (Payne 1981).

Success of Reintroduction Programs

Rapid increases in beaver population densities are characteristic of areas where the species is reintroduced following expatriation. This population growth is due to several

factors, of which the high reproductive rate of the species may be the most important. Females begin to reproduce in their third year and continue to do so into their tenth year, usually producing two offspring per year. Young are usually forced out of the lodge at two years of age and will travel up to 16 km from their birthplace to begin a colony of their own (Johnston & Naiman 1990a). A single female therefore has the potential to populate many square kilometers of suitable forage area with her offspring. Another factor important in this population increase of beaver is the decline (and in many cases expatriation) of the chief predator of beaver, the gray wolf (*Canis lupus*). The gray wolf was a formidable predator of beaver prior to the arrival of Europeans, but its decline has left beaver populations unchecked (Ringelman 1991).

It could also be reasoned that reintroduced beaver populations were initially exposed to high-quality habitat. In the absence of beaver, trembling aspen forests have developed unchecked along water courses, thereby creating optimal conditions for beaver reinvasion. Johnston & Naiman (1990a) suggest that the rapid rise in beaver populations following their reintroduction is directly related to the amount of optimal habitat now available. They studied beaver reintroduction in Voyageurs National Park, northern Minnesota, where the species was reintroduced in the 1930's. Aerial photographs from 1940 to 1986 were used to study the rise in and spread of beaver populations. They found that early increases in the population matched the rate of occupation of available habitat. Population densities remained low since there was extensive radiation from the introductory site to all surrounding suitable sites. Dam construction along streams was extensive. Only when all of the available sites were occupied did the beaver density within a given area increase. In 1940 there were 71 beaver pond sites and approximately 50 colonies in the 294 km² study area, but by 1972 this number had increased dramatically to 688 ponds and 278 colonies (Johnston & Naiman 1990a). A combination of high reproductive success, extremely advantageous habitats, and few predators likely promoted this invasion.

Alteration of aquatic systems by beaver activity

The presence of beaver changes the chemical, physical and biotic states and dynamics of a stream (Ringelman 1991; Broschart et al. 1989; Naiman & Melillo 1984; Hall 1957; Naiman et al. 1988; Naiman et al. 1986; Naiman et al. 1984; Smith et al. 1991; Johnston & Naiman 1990; Naiman 1988; Neff 1957). Naiman et al. (1988) proposed that beaver modify the stream ecosystem in a hierarchical manner. The species first alters stream morphology and hydrology by felling trees and constructing dams, creating a heterogeneity landscape of riparian wetlands and flooded forests. Beaver dams impede waterflow rates, leading to the retention of sediments and organic matter in the pond. The associated stream flora and fauna is affected by changes in water chemistry and stream nutrient cycling (Smith et al. 1991; Naiman et al. 1988; Naiman et al. 1986).

Changes in Hydrology

Alteration of the morphological and hydrological structure of a stream is perhaps the most obvious result of beaver occupation. Particularly apparent is the increase in water surface area associated with beaver dam construction. Impoundment of water can result in up to a hundred-fold increase in the volume of water within the ecosystem (Naiman et al. 1986). Neff (1957) reported that the surface area of water in some valleys increased 81-fold as a result of beaver activity. Impoundment also impedes the flow rate of water at a particular point along the stream course. In the Chavez Creek watershed of Colorado, beaver dams reduce the rate of stream flow by an order of magnitude (Neff 1957).

Increased surface area of water may provide increased wetland habitat for waterfowl (Ringelman 1991). In a two-year period, Neff (1957) found that 17 ducks had been raised

in beaver ponds while observing none in areas where beaver were not present. The benefits of water retention on waterfowl populations is expected to be most pronounced north of 40° latitude, as this represents the zone of summer breeding of waterfowl (Ringelman 1991). Another biotic factor affected by beaver activity is the fishery. In 1955 approximately 2,000 eastern brook trout (*Salvelinus fontinalis*) were fished out of the beaver ponds in the Chavez Creek watershed. By contrast, only two small trout were found in the valleys of the watershed lacking beaver (Neff 1957).

The flooding of areas adjacent to a stream bed may impact on several tree species that are not usually exploited by foraging beaver. Hall (1957) found that beaver significantly reduced lodgepole pine (*Pinus contorta*) abundance by the associated flooding caused by dam construction. Smith et al. (1989) demonstrated that the construction of dams also results in the regional flooding of areas that would otherwise dry out during the late summer months. This may result in the death or reduction in the growth of species normally associated with drier soils.

Changes in Invertebrate Communities

A number of studies have examined the response of invertebrate communities to beaver activity (Naiman et al. 1986; Naiman et al. 1988; Naiman et al. 1984; McDowell & Naiman 1986; Smith et al. 1991). Changes in species composition and density of invertebrate communities in the Pancake-Hall Creek, Adirondack Mountains, New York were examined by Smith et al. (1991). They examined three locations: immediately upstream of a beaver pond, immediately downstream of the beaver dam, and 250 m downstream. Sites immediately downstream of the dam had a lower species richness but a significantly higher density of invertebrates, primarily in the Diptera family. The 'collector' and 'gatherer' functional feeding groups were most common, together with predators. This was thought

to reflect a downstream increase in the amount of benthic organic matter, particularly woody decomposing particles from the dam wall and particles created by beaver foraging and feeding (Smith et al. 1991). The authors speculated that the decline in abundance of other functional feeding groups was a response to increased acidity of the water, which enhances the release of trace metals from the pond sediments.

Naiman et al. (1988), in an examination of the dynamics of beaver pond invertebrate communities, proposed that 'pond' taxa eventually replace 'running water' taxa in response to decreased water flow rates and increased deposition of fine sediments. Like Smith et al. (1991), they found an increase in the importance of 'collector' and 'predator' functional feeding groups at the expense of 'shredders' and 'scrapers'. Specifically, net-spinning caddisflies, blackflies and mayflies were replaced by dragon fly larva, tudificid worms and small filtering clams (Naiman et al. 1988).

Changes in Stream Nutrient Dynamics

Naiman & Melillo (1984) examined the nitrogen budget of a second-order stream associated with a pristine watershed in Minnesota. They found that areas of the stream associated with beaver activity accumulated 103x more nitrogen than areas in which beaver were absent, primarily in the organic matter sediment of the beaver pond. Beaver ponds contained 125 kg/m² of sediment, compared to only 1 kg/m² in the riffle. Nitrogen content of inorganic soil was not different between the pond and riffle, however. Naiman & Melillo (1984) suggest that the high nitrogen content of the pond sediment organic matter increases plant nitrogen availability. In a later study, Johnston and Naiman (1990c) found that the total nitrogen availability to plants was tripled in regions of active beaver occupation.

No significant differences were found in the dissolved organic carbon (DOC), particulate organic carbon (POC), or sediment concentrations of water entering and leaving a beaver pond (Naiman et al. 1986). There is however considerable accumulation of organic matter within the pond itself (Naiman et al. 1986). Beaver impact on the dynamics of the carbon cycle through their foraging and feeding, specifically by creating organic particles and defecating. This high sediment load has the ability to lower the level of dissolved oxygen in the pond water. This effect is thought to be short-lived, however, since the water is re-oxygenated as it flows over the dam top (Smith et al. 1991).

Beaver and Vegetation Dynamics

Several studies have examined the response of vegetation to beaver foraging activities in the regions surrounding a dam (Neff 1957; Naiman 1988; Naiman et al. 1988; Naiman et al. 1986; Barnes & Dribble 1988; Johnston & Naiman 1990a). An early study by Neff (1957) at the Chavez Creek watershed, Colorado found that beaver strongly influence the ecology of small stream valleys in the regions of their lodge through their dam building and tree felling habits. The study revealed that forage production in areas inhabited by beaver was significantly lower than in adjacent unoccupied areas. Production of willows was much higher in the occupied valleys, however.

Beaver absence after a given period of occupation can also affect the surrounding vegetation. Dam abandonment is generally associated with depletion of the supply of aspen (*Populus tremuloides*) near the pond. Beier & Barrett (1987) proposed two explanations for beaver abandonment in a California study: (a) the physical characteristics of the pond and stream valley become unsuitable; or (b) foraging resources are depleted. Beaver relocation is often to a site upstream having an extensive supply of aspen (DeByle & Winokur 1985; Beier & Barrett 1987; Naiman et al 1988).

Dynamic Vegetation Change in Beaver Ponds

Without a continual cycle of beaver dam repairs, the first spring freshet will usually result in a dam breach and consequent release of the contained water. This exposes a mudflat which undergoes an initial change from a wet-sedge meadow to one dominated by dry grasses and woody species (Naiman et al. 1988; Graham 1963). These 'early' plant communities provide large mammals such as moose, elk, and deer and smaller herbivores with an abundance of forage.

Although the role of the seed bank in directing vegetation change has been examined in a variety of habitats (e.g., prairie marshes, van der Valk & Davis 1978; Galinato & van der Valk 1986; Wienhold & van der Valk 1984; salt marshes, Hutchings & Russell 1989; lake shores, Keddy & Reznicek 1986, Leck & Simpson 1987), there are no comparable studies for beaver pond ecosystems. Several studies have demonstrated the importance of the seed bank on vegetation processes in prairie wetlands following a draw-down (e.g., van der Valk & Davis 1978, Welling et al. 1988), which is in many ways similar to the situation following beaver dam abandonment. However, studies dealing with vegetation change caused by beaver activity have generally focussed on the forested area surrounding an abandoned pond, and have largely ignored changes within the wetland itself (e.g., Barnes & Dribble 1988, Beier & Barrett 1987, DeByle & Winokur 1985). Those studies that have discussed changes in the wetland itself consist of anecdotal accounts (e.g., Neff 1957, Graham 1963, Naiman 1988).

Forest Dynamics

Masslich et al. (1988) found a significant reduction in the number of mature aspens in the region associated with beaver. However, overall aspen density in sites occupied by beaver was approximately five times higher than in areas without beaver (15,800 stems/ha vs. 2,980 stems/ha). This reflects the increase in aspen suckering stimulated by beaver foraging habits. Because the extensive aspen root system remains intact, aspen sucker growth is rapid compared to establishing seedlings of other species (Cook 1983; DeByle & Winokur 1985; Gese & Shadle 1943). DeByle & Winokur (1985) state that the removal of above-ground aspen biomass (by fire, beaver foraging and other factors) stimulates the release of primordial root tissue and the development of suckers, as long as the transverse roots are not damaged. Sucker densities to 50,000 shoots/ha have been observed, with the roots involved in this process occurring up to 15 meters from the parent tree (Masslich et al. 1988). Destruction of the transverse roots significantly lowers the likelihood of aspen regeneration. Aspen seeds do not germinate well in beaver meadow sites since the germination requirements of the species include bare mineral soil, full light, and dry conditions (Mitton & Grant 1980; Kittredge 1938; Gese & Shadle 1943; DeByle & Winokur 1985). Hall (1957) suggests that fire may create the conditions necessary for aspen germination, particularly if the fire burns away the organic layer to expose mineral soil.

Beaver aspen consumption has been reported to be as high as a tonne per year per pond (Naiman et al. 1988), and may lead to local expatriation of trembling aspen (particularly if the sucker shoots are also eaten). Beier & Barrett (1987) demonstrate local extinctions along 4-5 % along Truckee River Basin stream courses in northern California. They found that beaver foraging affected not only trembling aspen (*Populus tremuloides*) populations, but balsam poplar (*P. balsamifera*) and cottonwood (*P. trichocarpa*) stands as well.

The total area of forest affected by beaver is dependent upon their foraging patterns. Typically, beavers travel from between 100 to 200 m from the pond edge in search of aspen, the exact distance being largely dependent on the slope of the bank (Hall 1957; Masslick et al. 1988; Barnes & Dibble 1988). Johnson & Naiman (1990b) found foraging distances of only 35 to 45 m from the edge of a pond near Duluth, Minnesota. Harvesting by beaver in this forage zone has resulted in a decrease from 29.9% to 8.0% relative density over a six year period. Each beaver fells an average of 1300 kg of woody biomass each year.

The edge of a foraging zone may represent a dynamic boundary in which trembling aspen is cleared from within the zone when beaver are present. Trembling aspen stands would then occur only at some distance from watercourses. Beaver would then abandon the site, allowing aspen to reinvade areas closer to the stream (mostly by suckering) until beaver return to harvest again. When beaver are expatriated from a site, however, aspen stands are able to permanently encroach upon the stream edges. Reintroduction of beaver into many areas is again leading to the development of a dynamic forest vegetation boundary along watercourses in the boreal forest. Few studies have examined the effect of beaver on forest dynamics, however (Johnston & Naiman 1990b, 1990c).

The large economic potential associated with trembling aspen forests could be threatened by beaver occupation. Gullion (1986) states that in a single year a beaver colony can remove up to \$200,000 worth of aspen trees.

Early Models of Vegetation Dynamic in Beaver Habitats

Graham (1963) proposed that two vegetative routes of vegetation change exist, with the specific route taken being determined by the beaver population densities and duration of site

occupation. One route occurs when beaver population densities are high enough that continued consumption of aspen shoots will over time exhaust the root stores. As a result, few if any aspen trees will result from root suckering, and the area will come to be dominated by bracken ferns and grasses (Hall 1957, Graham 1963). Such a vegetation may be maintained since such areas generally possess characteristics which differentiate them from other stretches of the river channel. Specifically, the soils are often nutrient rich, and the water table tends to remain high. In addition, the ample supply of grasses and sedges promotes herbivore grazing and browsing which discourages invasion by trees. In some cases, conifers may eventually invade the site since they are not exploited to the same degree as aspen (Graham 1963). This condition is of course not static, and is at risk of being disrupted by a major event such as fire.

The second route of vegetation change occurs when beaver population density is relatively low. In such cases, aspen suckers will develop and encroach upon the edges and sides of the former pond through vegetative propagation. Dispersal of aspen by seed is expected to be less important since the edaphic conditions of the wet meadow are not conducive to the germination and growth of aspen seedlings (Graham 1963; Walker & Coupland 1970).

Naiman's Model of Vegetation Dynamics in Beaver Habitats

Naiman et al. (1988) have suggested a dynamic model that contrasts with the theories established by Graham (1963). They propose that beaver activity results in multi-

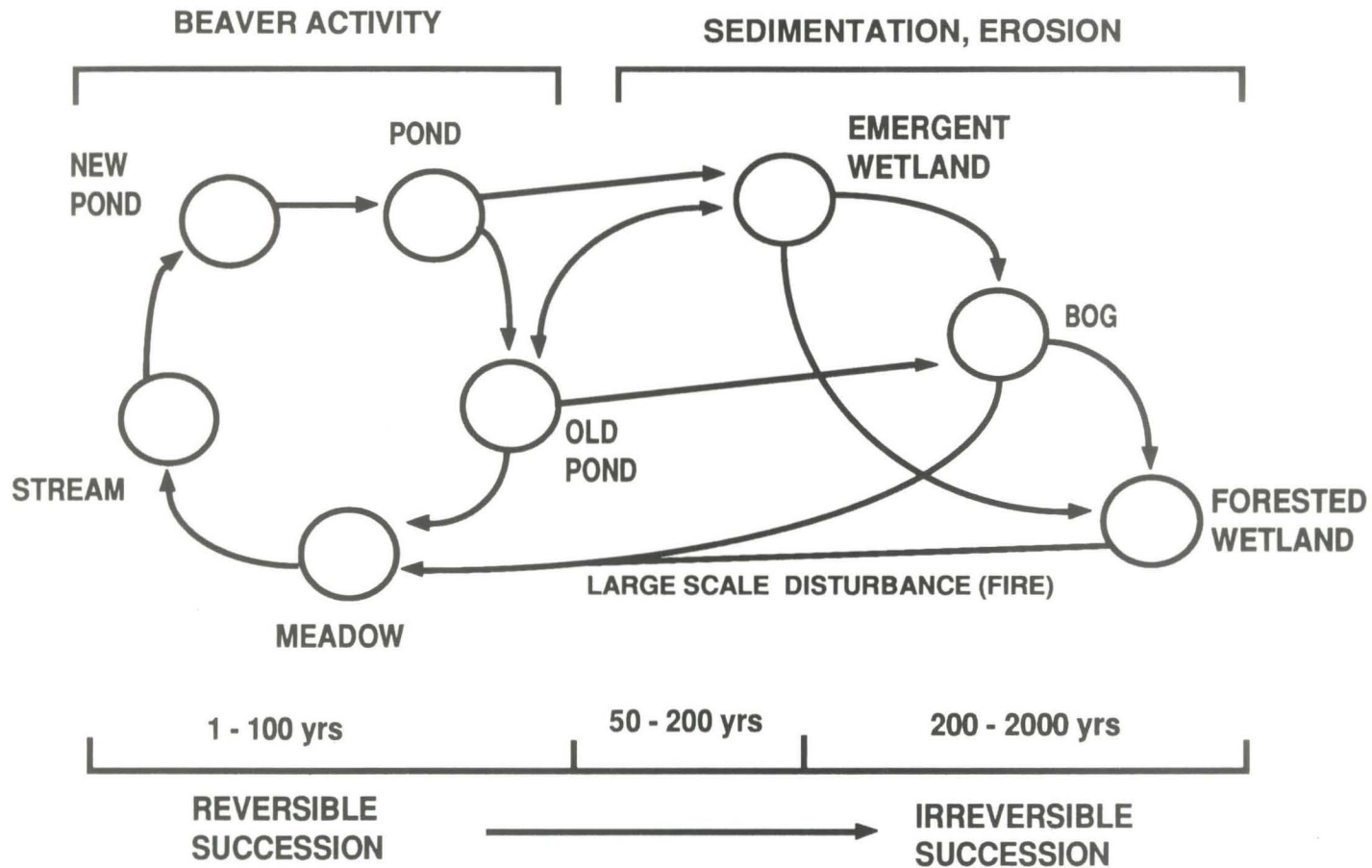


Figure 1.4 The beaver - meadow complex and its multisuccessional pathways (after Naiman 1988).

successional pathways which alter the landscape for centuries. Their model recognizes a long-term process that exists in two phases, each operating on different time scales (Figure 1.4). Initially there is a recognized beaver-meadow complex, in which a site moves from pond to meadow after abandonment, and reverts again to pond status once the site is recolonized. This condition is dependent on the activities of the beaver colony, but usually occurs within a time frame of <100 years. This phase is somewhat analogous to the dynamics model for prairie marshes proposed by van der Valk & Davis (1978), but with the cycle dependent on beaver activity rather than climate (flood-drought cycles). The time scale for the second phase is much greater in duration (Fig. 1.4). An emergent wetland can arise as a result of beaver activity when forage is so abundant that beaver can remain in the region for extended periods, ensuring that the pond does not drain for a considerable length of time. Given this condition, a boreal emergent wetland may develop at the site. With sedimentation, a forested wetland dominated by conifers may eventually replace this wetland. Naiman et al. (1988) suggest that such long-term processes could be reverted to the initial phase by a large-scale disturbance such as fire. Following the fire, aspen could establish in the stand by seed, beginning the cycle anew. Thus the two phases undergo a cyclical process that is dependent on several factors, of which beaver activity is only one (Naiman et al. 1988).

All of the above cycles can be altered by human intervention. Sites where man breaches a dam are likely to contain ample supplies of aspen, so that beaver will return to repair the breach. This will reflood the exposed mudflat, and the site will revert to an aquatic habitat. Repeated artificial breaching by man may disrupt the procession of vegetative communities which would normally develop after a natural breach, since the plants which began germinating in the mudflat would be killed by the flooding associated with the beaver reoccupation. This may exhaust the seed bank by dwindling the seed supply over time.

Domesticated animals may also alter the proposed cycles by consuming aspen suckers and so preventing aspen regrowth (Beier & Barrett 1987).

In studies of 'natural' ponds (i.e. those not occurring as a result of beaver activity), van der Valk & Davis (1978) have suggested that early-germinating species, which appear in the first or second year following drawdown, are present in the seed bank before the pond drains. This may be true of beaver pond seed banks as well. Studies are required to either support or refute this hypothesis, however. The composition of a pond's seed bank is expected to change over time once a drawdown occurs. Wind-born seeds will be deposited and nearby plants will invade by vegetative propagation. Although present, it is expected that some species found in the seed bank will not be found in the vegetation that ensues, either because conditions or requirements necessary for germination are not be present or because competition for space or nutrients suppresses germination and/or establishment (van der Valk & Davis 1978; van der Valk 1981).

Summary

1. Beaver are a key component of a wide variety of North American ecosystems. In the boreal forest they may be considered a 'keystone species' (Naiman et al. 1988), at least in areas along watercourses.
2. Beaver considerably alter ecosystems by changing the stream (both physically and biologically), the area flooded, and the forest within the foraging zone.
3. The degree to which animals affect ecosystems has only recently attracted the attention of contemporary ecologists (e.g., Naiman 1988; Huntly & Inouye 1988). Early North American explorers reported a continent that had skies full of migratory birds, lakes and

rivers with great abundances of fish, and forest and plains covered with fur-bearing mammals (Naiman 1988). The role that these animal populations had on the dynamics of ecosystems will never be fully known, but by studying less disturbed areas in North America we can obtain some sense of their importance. The study of vegetation dynamics in regions flooded by beaver is one area deserving of further study.

Chapter 2 Study Site Description

2.1 Introduction

The study area incorporates the upper reaches of the Little Saskatchewan River from its headwaters at Whitewater Lake to where it empties into Lake Audy. The river flows out of the southern end of Lake Audy and continues through a wide, deep valley until it flows into the Assiniboine River near Brandon, Manitoba. The upper reaches of the river are characterized by a high population density of beaver. Between Lake Audy and Whitewater Lake the river includes a large number of full and abandoned ponds and meadows. Jackfish Creek, which flows into Lake Audy from the north-east, also has high population densities of beaver and large numbers of beaver dams and meadows. However, this study only examined beaver ponds and meadows along the Little Saskatchewan River, as it has a relatively conservative stream morphology. By contrast, the course of Jackfish Creek has changed through time making the interpretation of aerial photographs difficult.

Local Area Geography

The upper reaches of the Little Saskatchewan River are situated on the western portion of the Manitoba Escarpment Highland Plateau (RMNP 1979). Whitewater Lake (50°48'N, 100°24'W) is shallow and has a surface area of $\approx 11.5 \text{ km}^2$. Lake Audy (50°45'N, 100°15'W) is deeper and has a surface area of $\approx 5 \text{ km}^2$. Between the two lakes the river is approximately 15.4 km in length (Fig 2.1). The total vertical relief along this length is only 30 m (600 m ASL at Whitewater Lake, 570 m ASL at Lake Audy).

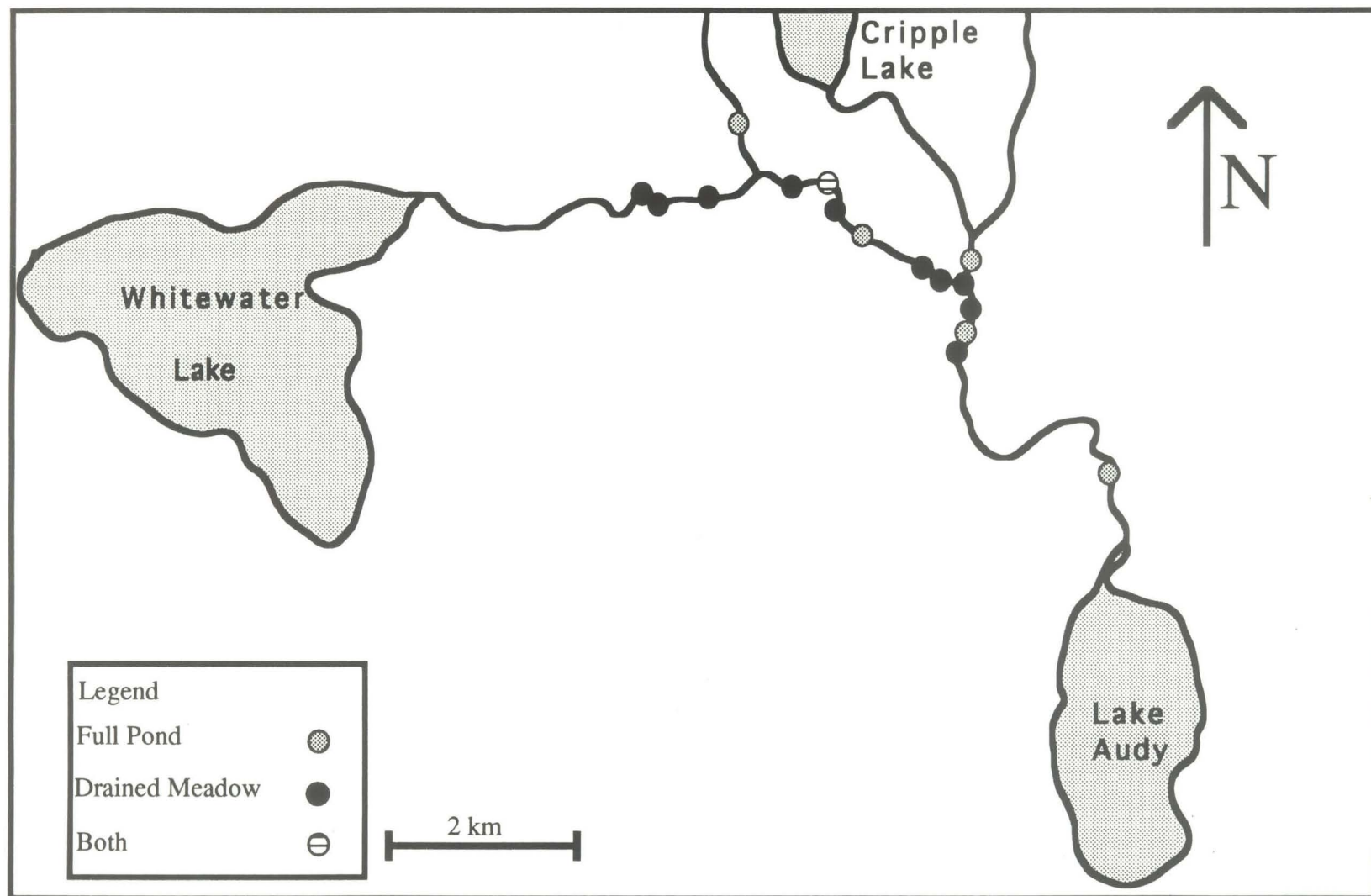


Fig 2.1. Little Saskatchewan River from Lake Audy to Whitewater Lake. The full ponds were sampled in the May of 1991, the drained ponds in August of 1991.

The beaver pond-meadow sites surveyed in this study extended from approximately 2.5 km downstream from Whitewater Lake to approximately 2 km upstream from Lake Audy, i.e. a 10.9 km length section of the river. Closer to Whitewater Lake the river valley is ≈ 75 m in width and has steep sides. Further downstream the river valley widens up to 250 m, and the riverbank has a very low slope.

Local Geology and Soil

The Little Saskatchewan River area (Moon Lake Landform, Fig 2.2) is underlain by Odanah Shale of the Riding Mountain Formation. This landform is defined as hummocky to undulating stagnation moraines. The dominant soils of the area are Orthic Gray Luvisols, although areas along the river course of Organic Mesisols (RMNP 1979). The dominant vegetation is mixed trembling aspen-white spruce forest, and trembling aspen forest. Two land types are recognized for the area, Moon Lake 1 (ML1) and Moon Lake 2 (ML2). The majority of the study sites occur within ML2, which is characterized by imperfect to poor drainage. Soils of wetter areas are Orthic Humic Gleysol, while those of drier areas are A-Orthic or Dark-Gray Luvisols. Soil texture ranges from loam to a loam-sand-clay mix. ML1 is characterized by Orthic Gray to Dark-Gray Luvisols with some Brunisolic Gray Luvisols. Both landform are moraine in nature with areas that are undulating and hummocky. These to land forms are representative of aspen and spruce areas.

Local Weather

Precipitation and temperature data for the period May-October 1991 (the year the sites were sampled) are presented in Fig 2.3. This data were collected at Wilson Creek, which is approximately 32 km to the North - East of the study area.

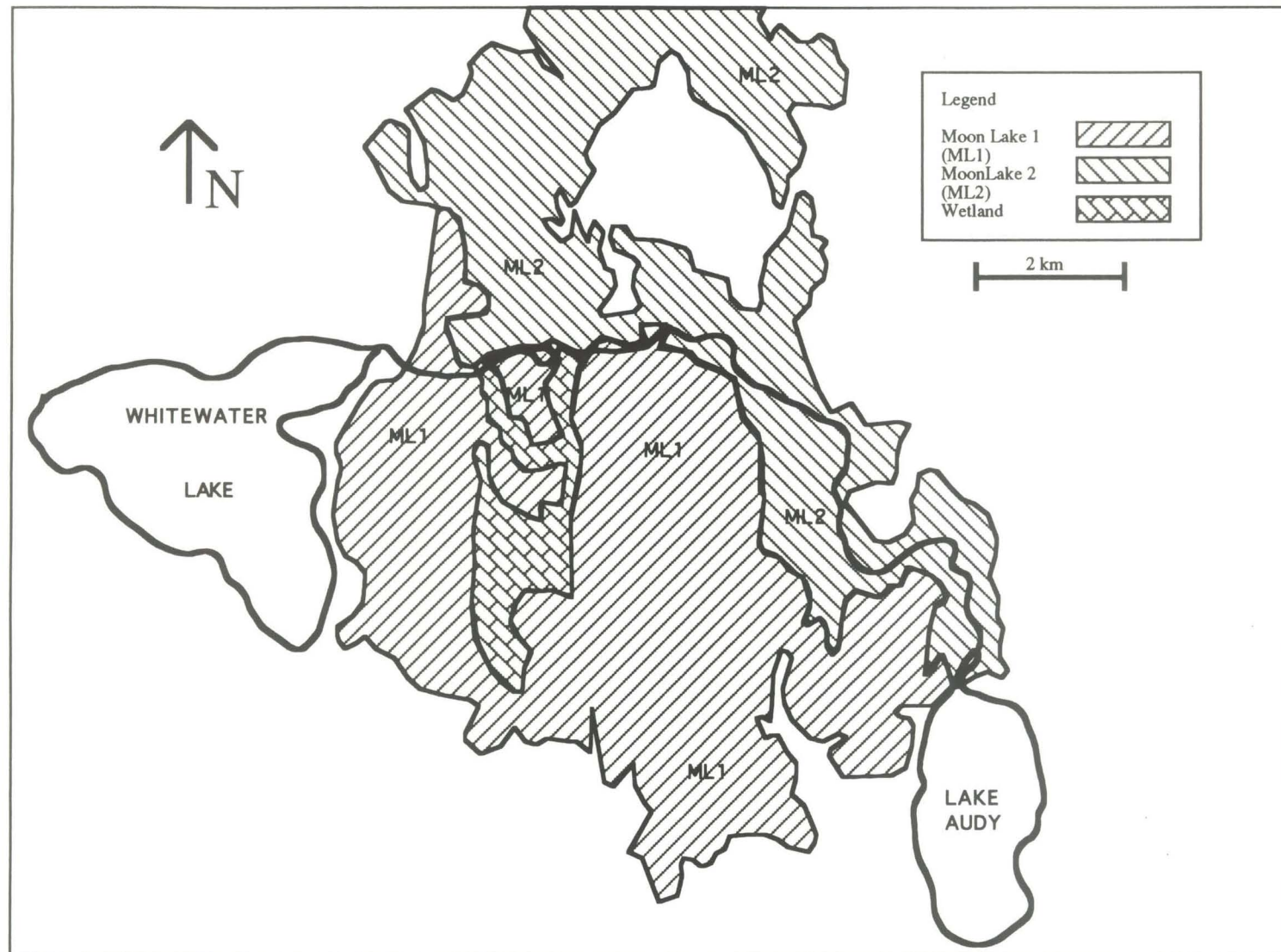


Figure. 2.2 The location of three different landforms along the Little Saskatchewan River. The river from Whitewater Lake to Lake Audy is within the Moon Lake formation. There is also a small area of wetland depression. (After RMNP 1979).

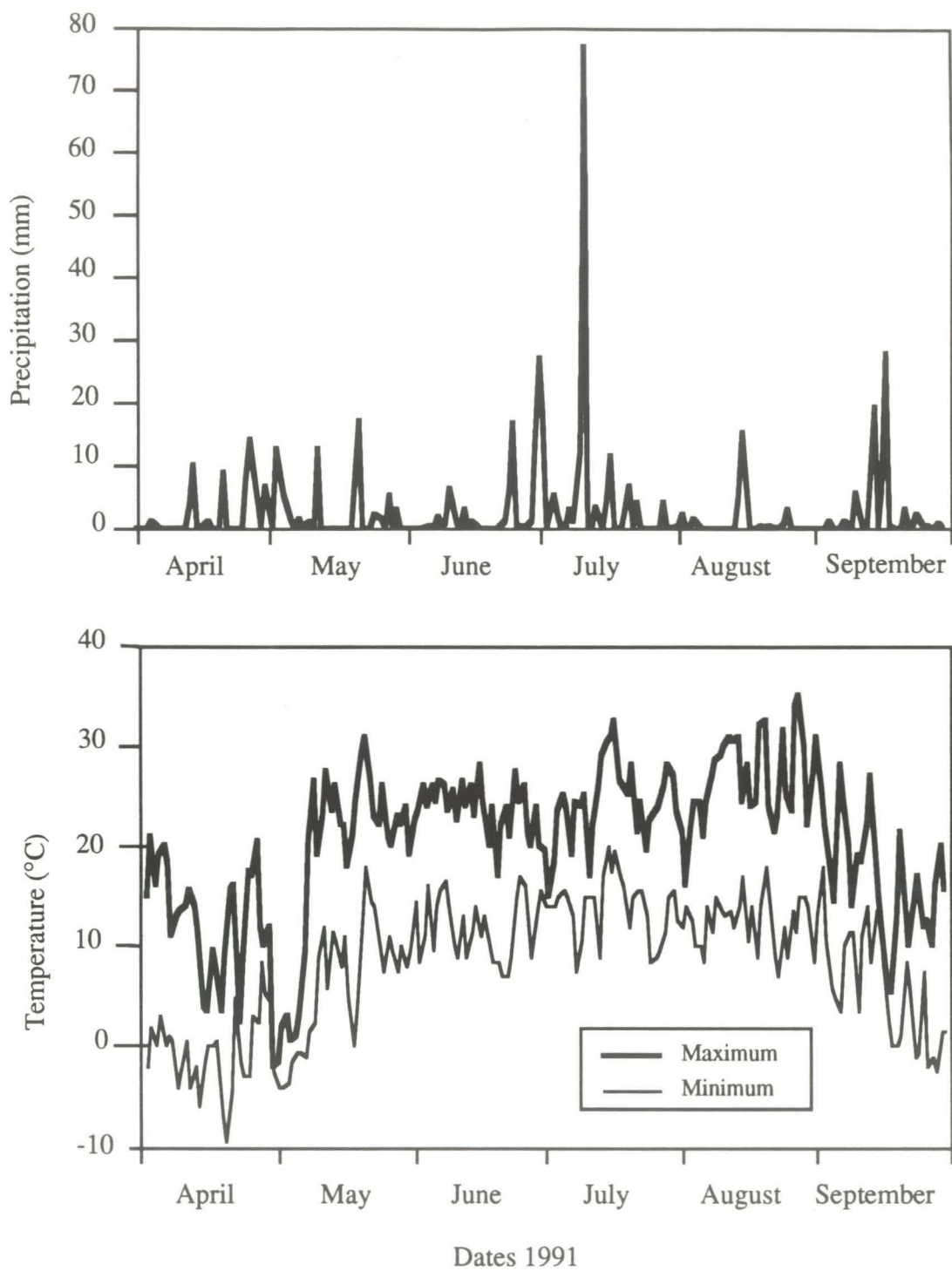


Figure 2.3 Total daily precipitation and maximum/minimum daily temperature over the 1991 growing season (1 April - 31 September). Data from Environment Canada climate station, Wilson Creek, Manitoba.

Long-term mean temperatures at Wasagaming indicate that May through October have daily means above freezing, with the highest mean in July (Fig 2.4a). Long-term mean precipitation shows much more variability than that of temperature (Fig 2.4b). The period from October to April is the driest, though in all months a minimum of 20 mm of precipitation falls. The long-term means for the wettest months, May to September, are high variability. June is the wettest month (averaging ≈ 10 cm precipitation) and shows the highest variability.

Hydrology

There is no flow rate station along the upper reaches of the Little Saskatchewan River. The most upstream station (M5F-01) is located "near Minnedosa" ($50^{\circ}21'28''\text{N}$, $99^{\circ}54'00''\text{W}$) and has a total drainage area of $2,620 \text{ km}^2$ (Environment Canada 1986). At this location a number of streams and tributaries have entered the river downstream from the Lake Audy inflow. The drainage area of the Little Saskatchewan River at the Lake Audy inflow is $\approx 210 \text{ km}^2$, or $\approx 8\%$ of the total drainage area represented by the flow recorder (Fig 2.5).

Yearly waterflow peaks in May (Fig 2.6), suggesting that snowmelt is an important contributor since the yearly precipitation peak does not occur until June. The actual peak flow does not always occur in May, however. In a twenty-two year period (1965-1986) the monthly maximum waterflow occurred 11 times in May, 8 times in April, and once each in June, September and October. Mean monthly flow rates for the period January 1965 to May 1992 are presented in Fig 2.7. Note that from January 1965 to January 1973 flow rates were only recorded during ice-free periods. In 1991, the year of the study, waterflow during spring and summer was relatively low. Observations in the spring of 1991 indicated

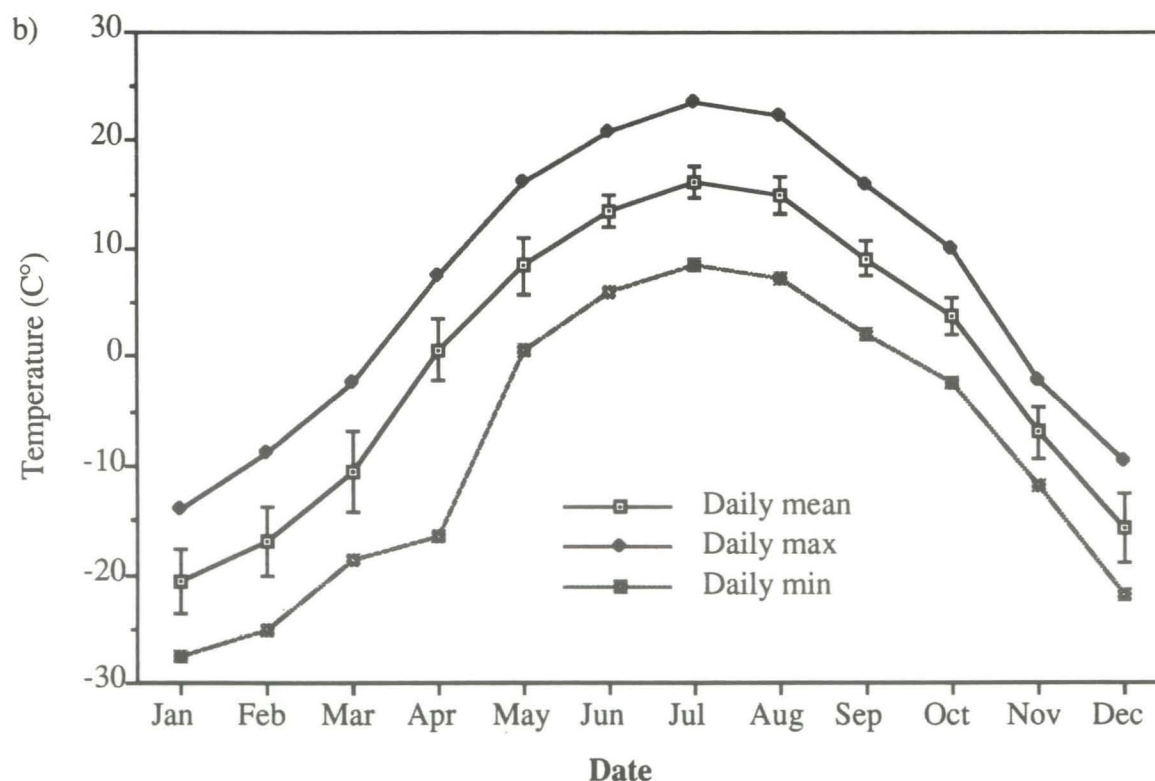
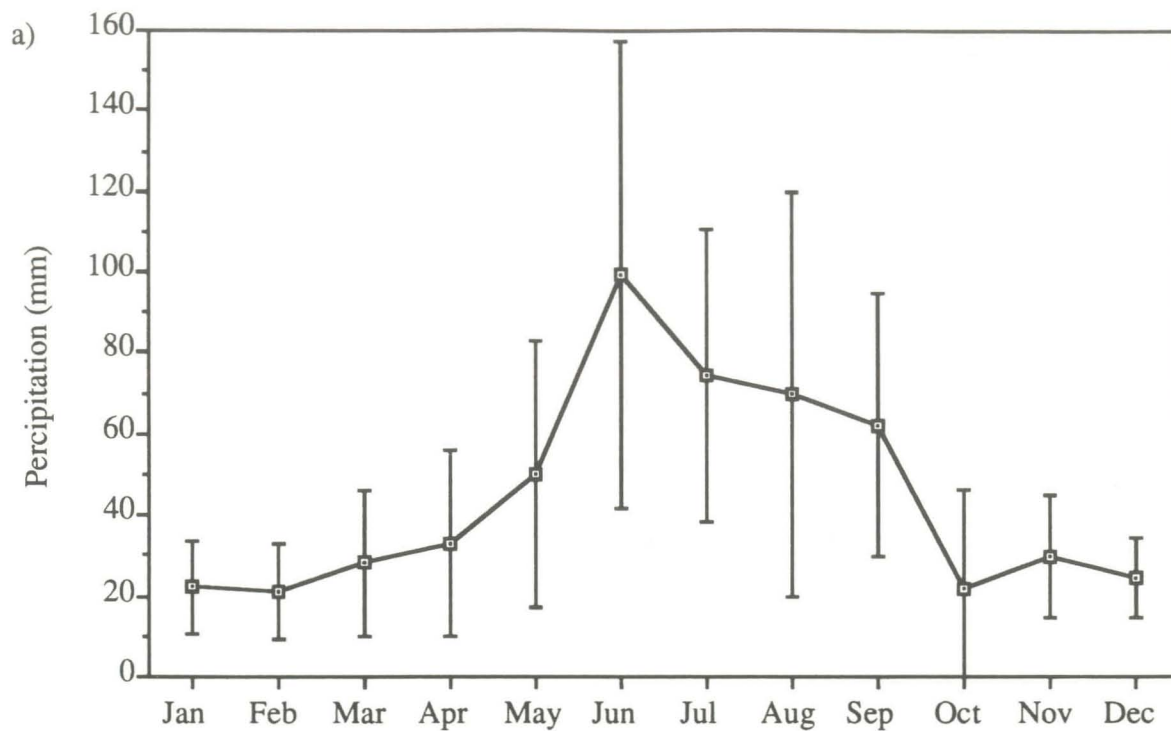


Fig 2.4a,b The 30 year average temperatures and precipitation for Riding Mountain National Park. Error bars represent ± 1 SD.



Figure 2.5 Little Saskatchewan River watershed. The area shaded in the upper left indicates the study area. The open circle indicates the location of the hydrometric station (M5F-01) that is used in the study (After Manitoba Natural Resources, 1987).

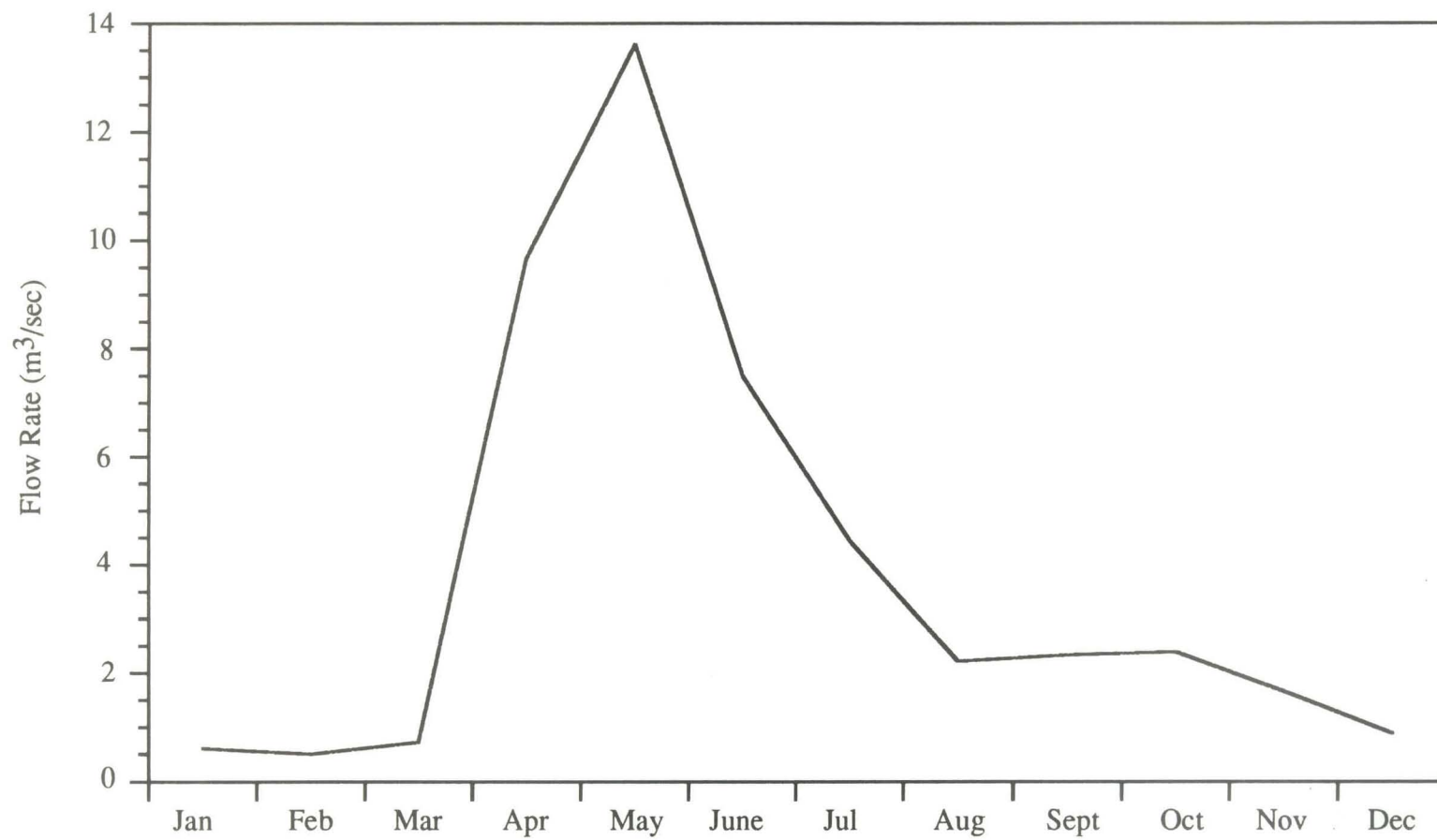


Figure 2.6 Average monthly flow rates (1960-1990) for the Little Saskatchewan River as recorded at the hydrology station 5MF-01.

limited flooding of areas upstream from breached dams. However, very strong flow and the flooding of areas behind breached dams was observed in May of 1992, a year of high spring waterflow. Water flows as high or higher than in the spring of 1992 have occurred nine times since 1965, most recently in 1986 and 1987 (Fig. 2.7).

Vegetation

The forests bordering the river valley are dominated by white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) (Fig 2.8). The shrub stratum is dominated by hazelnut (*Corylus cornuta*) and raspberry (*Rubus* spp.). Common forest understory species include wild sarsaparilla (*Aralia nudicaulis*), rice grass (*Oryzopsis asperifolia*) and tall bluebell (*Mertensia paniculata*). The plant community along the Little Saskatchewan River valley is defined as a non-forested wetland by Parks Canada. The dominant plant species include marsh reed grass (*Calamagrostis canadensis*), awned sedge (*Carex atherodes*), water sedge (*Carex aquatilis*), Canada thistle (*Cirsium arvense*), stinging nettle (*Urtica dioica* ssp. *gracilis*), shrub willows (*Salix* spp.) and mint (*Mentha arvensis* var. *villosa*).

Site Selection

A total of 15 beaver meadows (drained beaver ponds with a breached dam) and 7 extant beaver ponds were located using aerial photographs. Ponds were identified with a P and a number (e.g., P7), and meadows by a M and a number (e.g., M2). Each pond was visited and six were sampled for soil factors and soil seed bank. The seventh pond was not sampled since a large portion of its 'dam' was in fact a man-made gravel road bank. A total

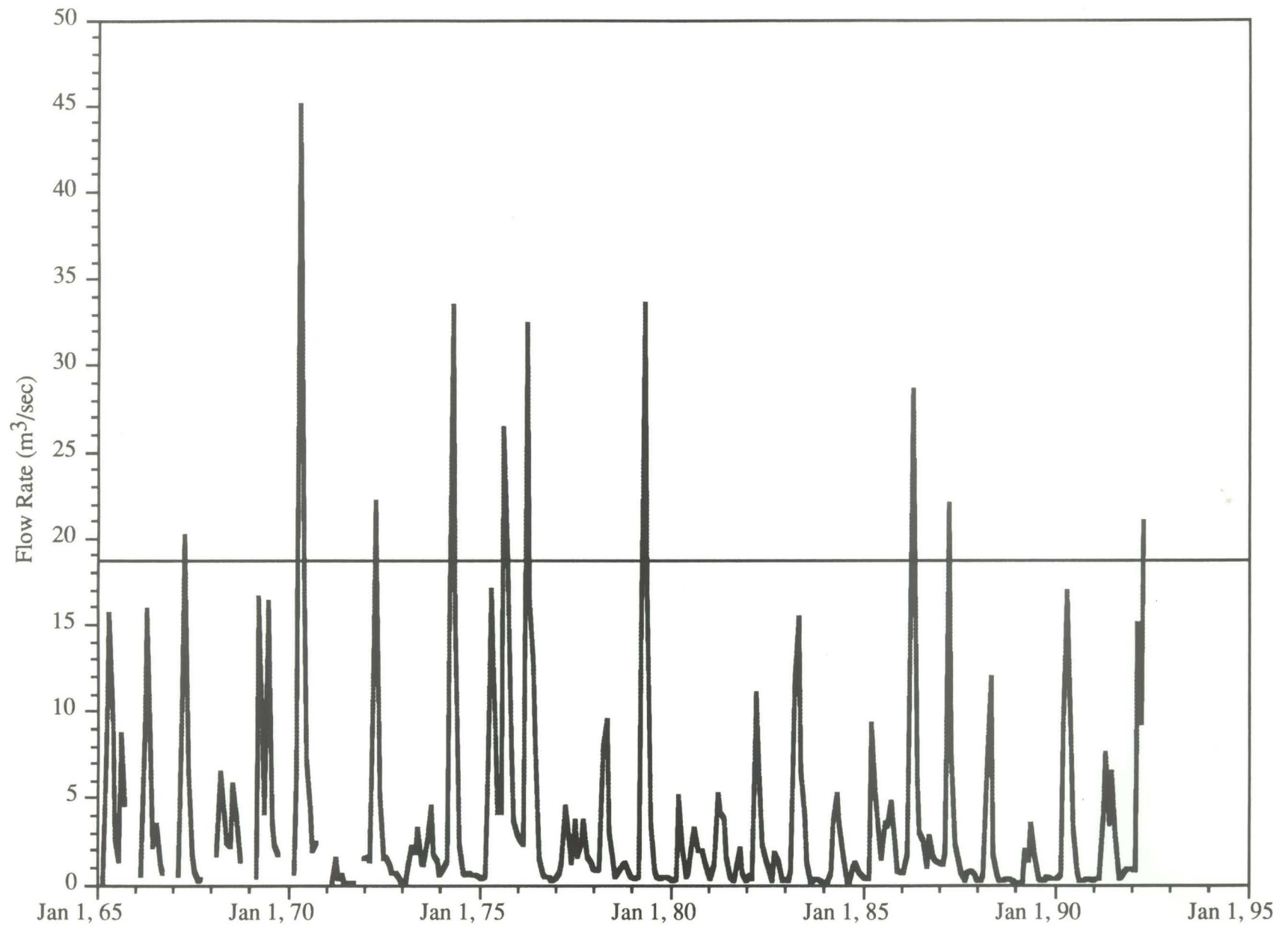


Figure 2.7 Monthly average flow rates for the Little Saskatchewan River.
Line indicates flow rate when water was observed backing up behind
breached dams in May 1992.

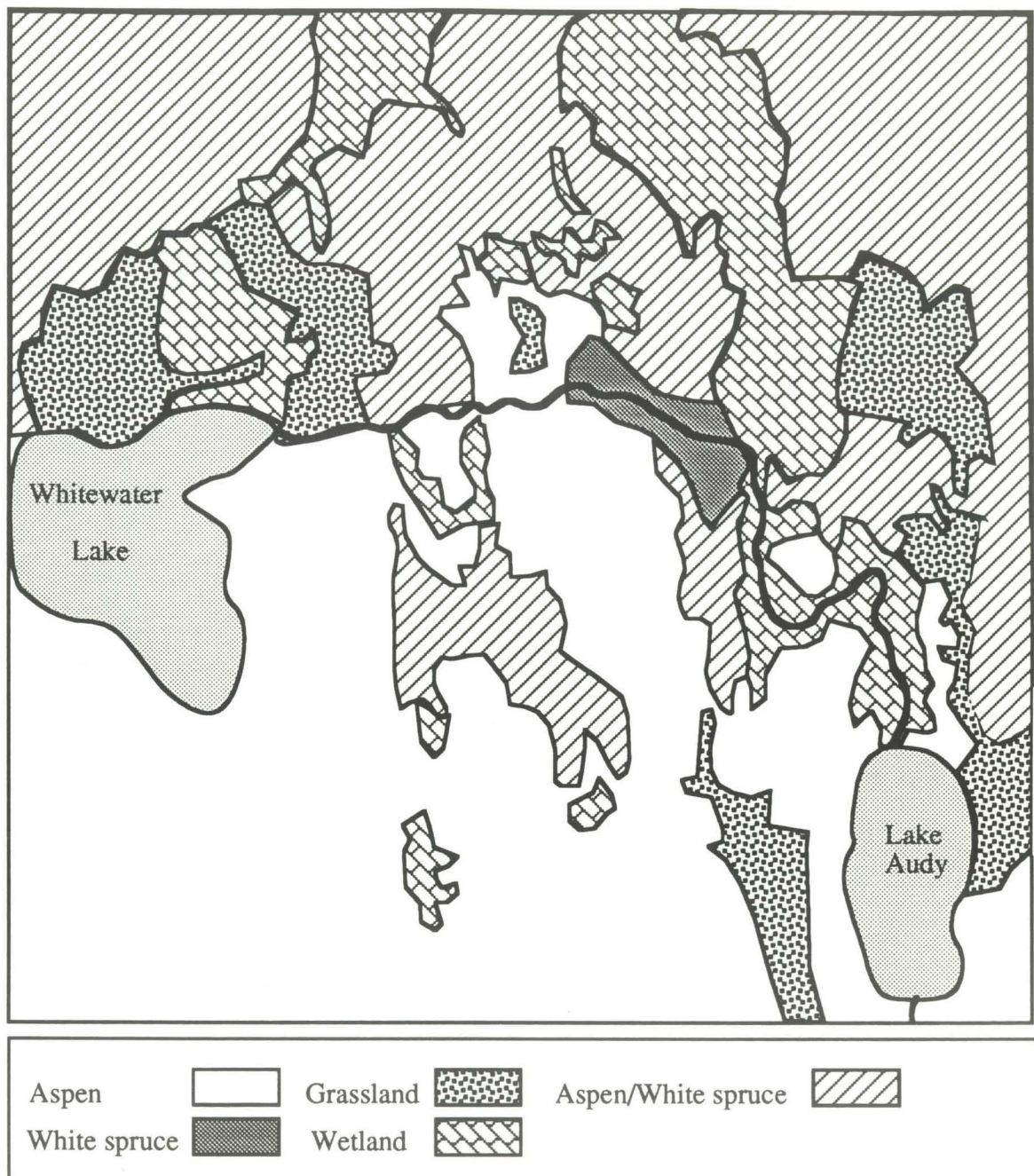


Figure 2.8 Dominant vegetation of Whittewater Lake / Lake Audy area of Riding Mountain National Park (from RMNP 1979).

of 11 of the 15 meadows were sampled for extant vegetation, soil factors, and soil seed bank. The remaining four meadows were not used for a variety of reasons. In two cases meadows were flooded in August 1991 by new dams constructed downstream. A third meadow was excluded since it occurred upstream of Long Lake road in a different landform type. The fourth meadow was excluded as it proved to be one of a series of meadows resulting from a single set of dams. As one of these meadows had already been sampled, it was decided not to sample the second one. More detail on each of the sites sampled is given in the following chapters.

Chapter 3 Soil Chemistry of Full and Drained Beaver Ponds

3.1 Introduction

Studies that compare the terrestrial vegetation of various regions must take into consideration the prevailing edaphic conditions, in particular the physical and chemical properties of the soil (Moore & Chapman 1986). Soil conditions such as pH and conductivity (as a measure of overall nutrient status) play an important role in determining the species composition and vegetation physiognomy of terrestrial plant communities. This is because plant species differ in their response to soil conditions, and show optimal performance at a given soil factor level and decreased performance at higher and lower levels of that factor (Crawley 1986). In some studies the null hypothesis is that variation in vegetation composition and structure is attributable to inherent variation in soil conditions (e.g., Jones 1991). In other studies, however, one wishes to demonstrate that soil conditions are similar throughout the study area in order that other factors affecting the vegetation can be examined and quantified. In such cases soil analysis is undertaken to ensure that sites are comparable to one another. If sites are to be compared, it must be demonstrated that variation in edaphic features is not confounding the results obtained.

This study focuses on obtaining a description of the soils of the Little Saskatchewan River valley, at the spatial scale of individual ponds and meadows along this river system. The uplands soils in this area are underlain by Odanah Shale of the Riding Mountain Formation. The dominant soils are Orthic Gray Luvisols with textures varying between loam and a loam/clay/sand mix. The available literature describes the riverine soils as being "organic in nature" (RMNP 1979), but specific information on organic content, pH, conductivity and other soil factors is lacking. Such information is required in obtaining an

understanding of the degree and extent of edaphic variation within the beaver pond-meadow network.

The objectives of this soil study are:

1. to describe and characterize the variation in four soil factors (organic content, bulk density, pH and conductivity) within each of the six study ponds.
2. to determine if there are any differences in the same four soil factors between the six study ponds.
3. to describe and characterize variation in five soil factors (organic content, bulk density, pH, conductivity and water content) within each of the eleven beaver meadows studied.
4. to examine and describe variation in these same five soil factors between the eleven beaver meadows.
5. to determine if there are any trends in the five soil factors with beaver meadow age.

3.2 Field Methods

Soil from full and drained ponds ('beaver meadows') were extracted using a soil corer. In the full ponds each soil sample was extracted using a 2 m length of polyvinyl chloride (PVC) pipe, 10 cm in diameter. Samples were taken from the ponds using waders or, when the water was too deep, from a small inflatable boat. Soil cores from the drained ponds were taken with a 10 cm diameter metal soil corer. In all cases soil cores were taken

to a standard depth of 10 cm. Each soil core was placed in a sealed and labelled plastic bag and stored in a cooler until they could be transported to a coldroom at the University of Manitoba (Department of Botany).

A transect was established along the dam top at each of the six full ponds and eleven beaver meadows. A sample site was established every 5 or 10 m along this transect, depending on the length. Longer dams were sampled every 10 m, small dams every 5 m. A second transect was located along the dam face with the same sampling methods. More transects were then established parallel to the dam 20 m, 40 m and in some larger ponds and meadows 60 m away from the dam. In each of the six full ponds a soil core was taken from each sample site. At two sample sites on each transect, an extra soil core was taken for soil chemistry analysis as opposed to seed bank determination (see Table 3.1). In the eleven beaver meadows, soil cores were taken from every third or fourth sample location along the transects. Each of these samples were used for both soil chemistry analysis and seed bank determination. The number of soil cores taken from each of the sites (by transect and meadow or pond) is summarized in Table 3.1.

Soil conductivity, bulk density, soil moisture and organic matter content and pH were measured for each soil core. For the beaver meadow soil cores, percent water in the soil was also determined. In all cases values were expressed on a per volume basis. It has been previously been demonstrated that expressing soil parameters on per volume basis is more ecologically informative than older methods which expressed values in terms of dry soil mass (Gosselink et al. 1984, Jones 1991). This is because plant roots 'interact' with a volume of soil, not the soil mass (Brady 1974). It follows that the concentrations based on volume of soil are of greatest ecological relevance (Burchill & Kenkel 1991).

Table 3.1 The number and location of soil cores removed from the field for chemical analysis.

Pond No.	No. Transects	No. Samples
1	4	8
2	5	10
3	4	8
4	4	8
6	4	8
7	4	8
Pond total	25	50
Meadow No.	No. Transects	No. Samples
1	5	19
2	5	18
3	4	9
5	4	12
7	4	13
8	5	19
11	4	18
12	4	13
14	4	12
15	4	16
p4	4	13
Meadow total	47	162
Total	72	212

3.3 Laboratory Methods

Bulk Density

All soils were dried in an oven for at least 24 hours at a temperature of 60°C. Soil bulk density (BD) was then determined by dividing the dry mass of soil by the soil volume (Brady 1974):

$$\text{BD (g/ml)} = \frac{\text{mass of dry soil (g)}}{\text{volume of sample (ml)}}$$

Once the bulk density was determined, the soil was ground using a Braun coffee grinder and passed through a 2 mm sieve. Particles larger than 2 mm were discarded, and all further analyses were based on the sieved soil fraction.

Organic Content

Soil organic content was determined using the combustible carbon method (McRae 1988). A known mass of drier, sieved soil (in all cases, approximately 10 grams) was randomly selected from each soil core and placed in a labelled beaker. The beaker was then placed in an 105°C oven for 24 hr to drive off any excess soil water. The soil was then placed in a ceramic crucible and massed. Each crucible was then placed in a muffle furnace and fired at 430°C for 18 hours. Upon completion of firing, crucibles were placed in a desiccator to cool. Once cool, the crucibles were removed from the desiccator and massed again. The organic content (%OM) of the soil is calculated as:

$$\%OM = \frac{[\text{mass of pre-fired soil (g)} - \text{mass of fired soil (g)}]}{[\text{mass of pre-fired soil (g)}]} \times 100$$

Conductivity

In non-saline soils, soil conductivity can be used as a general indicator of soil nutrient levels (Moore & Chapman 1986). There are some problems with this method of determining nutrient availability. The level of hydrogen ions can contribute a major proportion of total conductivity to the soils. However, as the soil in this area is neutral to basic in nature, the correction for hydrogen ions was not used (Moore & Chapman 1986). No testing was done on the soil to determine what elements were the major factor in the conductivity readings. As the soils of the area are not saline (RMNP 1979) and because my tests indicate that the soil is not acidic, it is assumed that the conductivity represents a measure of nutrient availability to terrestrial plants.

Soil conductivity was determined using a 1:5 (by mass) extract of dry soil to water. A conductivity probe (Radiometer Electrodes, model CDC104) was inserted into the extract and the conductivity value recorded from the connected meter (Analytical Instrument Science, model COND72).

Soil pH

Soils of the upper regions of the Manitoba Escarpment are of shale origin and therefore relatively alkaline (RMNP 1979). If soil is too alkaline (high pH), it may create nutritional problems for the plants as both macronutrient (e.g., calcium, magnesium, phosphorus) and micronutrient (e.g., iron manganese, zinc cobalt and copper) availability decreases above a pH = 7.0 (Brady 1974). High acidity has the same effect on availability of the macronutrients nitrogen, calcium, magnesium, phosphorus, potassium and sulfur, as well as micronutrients such as boron and molybdenum (Brady 1974). It is therefore important to know the range of pH that is found within the soils of the study site.

Soil pH was determined using the same 1:5 soil extract used to determine soil conductivity. A standardized pH probe and meter (Fisher Scientific, Probe model E-5C, Meter model 229) were used for determinations.

Soil Moisture

Soil moisture content of the soil was determined for the soil of the drained ponds only, as it was assumed that soils from the bottom of the ponds was saturated. Percent soil moisture (%SM) was determined as the percentage loss of mass of field soil when dried at 105°C for 24 hours (Brady 1974):

$$\%SM = \frac{[(\text{mass of wet soil (g)} - \text{mass of dry soil (g)})]}{[\text{mass of wet soil (g)}]} \times 100$$

3.4 Data Analysis

Data Structures

Sample sizes for the soil cores (by meadow or pond, and transect) are shown in Table 3.1. The soil information collected was structured in order to determine variation within each pond or meadow, and to compare soil factors across ponds or meadows. In addition, variation in soil conditions with meadow age was examined. To address these questions, the following data structures were created:

1. Ponds

- Separate analyses were undertaken for each of four soil factors: soil conductivity, bulk density, percent organic matter and pH.
- For each of the six ponds, variation in soil factors was assessed by comparisons made across transects. Four or five transects were defined for each pond:

Transect

1. Top of the dam (not underwater).
 2. Dam face, generally 2-4 m from the dam top (underwater).
 - 3-5. Increasing distances from transect 2 (underwater).
- Soil factors for the the six ponds were compared. Soil cores from a given pond were considered as replicates regardless of which transect they were taken from.

2. Beaver Meadows

- Separate analyses were undertaken for each of five soil factors: soil conductivity, bulk density, percent organic matter, pH and percent water content.
- For each of the eleven meadows, variation in soil factors was assessed by comparisons made across transects. As for the ponds, four or five transects (depending on areal extent) were defined for each meadow:

Transect

1. Top of the former dam .
 2. Lower dam face of each meadow, on the upstream side.
 - 3-5. Increasing distances from transect 2.
- Soils factors of each of the eleven beaver meadows were compared. As in the ponds, soil cores from a given meadow were considered as replicates regardless of where they were taken.
 - Comparisons were also made across age classes. In this case, replicate soil cores were those from a given age-class of meadow. There were five age classes (1, 6, 9, 21 and 22 years old).

Analytical Methods

1. Tukey Box-Plots

Box plots (Figure. 3.1) were used in all cases to summarize averages and ranges of the soil factors within a given transect, pond or meadow. Such plots include the median value and its 95% confidence interval, as well the the ± 1.0 and ± 1.5 interquartile ranges.

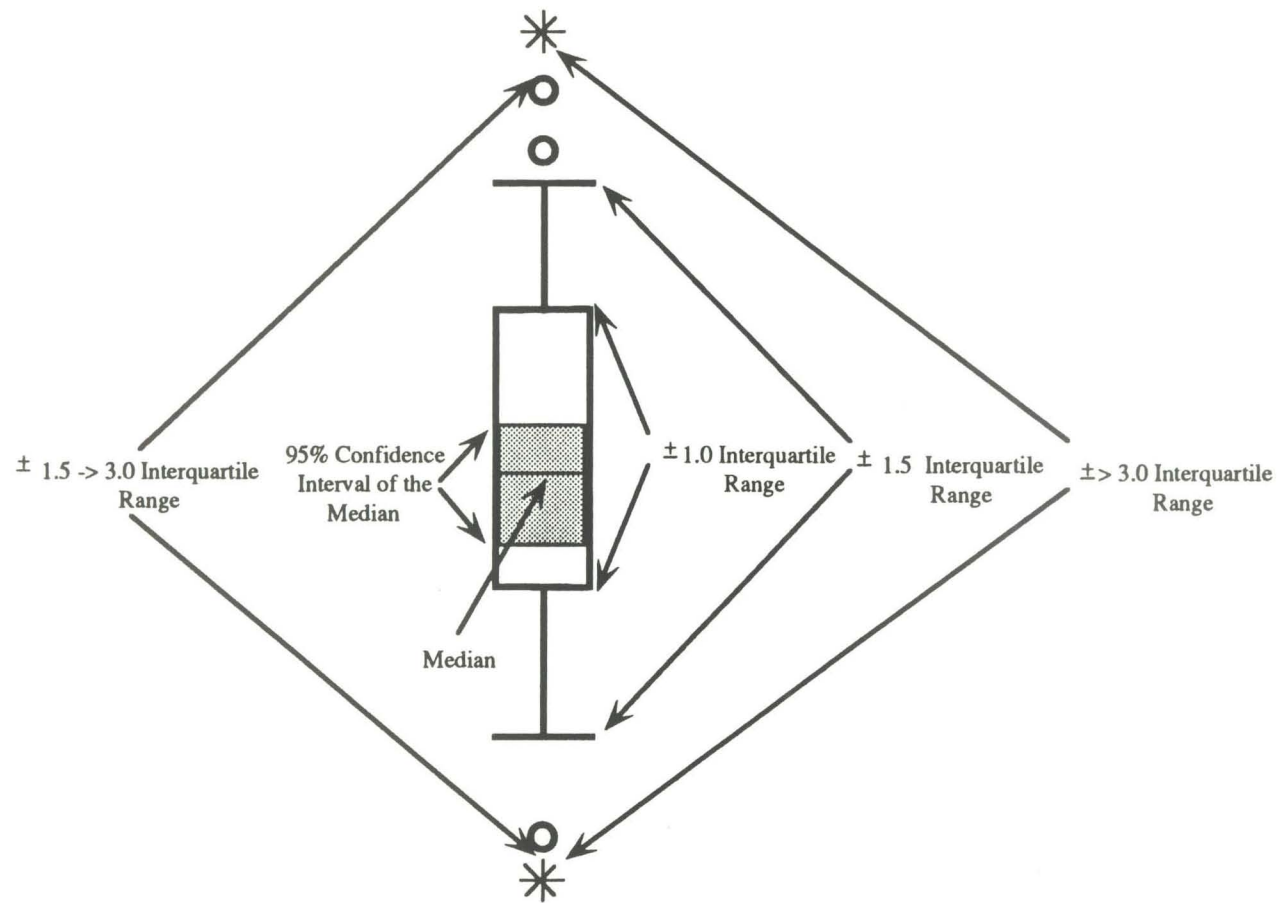


Fig. 3.1 Diagram of Tukey Boxplot with explanation. The rectangular box represents $\pm$ interquartile range, with the median indicated by the horizontal line, and the shaded area representing the 95% confidence interval of the median. T's extend from the box to the nearest point within ± 1.5 interquartile range. Circles and stars represent outliers within and beyond ± 3.0 interquartile range respectively. (from Emerson & Strenio 1983).

Outliers are represented by circles (within ± 1.5 -3.0 interquartile range) or stars ($> \pm 3.0$ interquartile range). Box plots were generated using the Data Desk® 3.0 exploratory analysis package.

2. One-way Analysis of Variance

Comparisons between transects of a given pond, or meadow, were performed using the standard one-way analysis of variance (Zar 1974, p. 133-139). In some cases the transects only consisted of two samples. For this reason some tests were done with all the same transect samples grouped together. In all cases, data were tested for normality and equality of variances. ANOVA's were performed to determine if age of meadow, or sample location affects any of the soil factor values. Analyses were performed using the Data Desk® 3.0 exploratory analysis package.

3. Two-way (Factorial) Analysis of Variance

Comparisons between ponds or meadows were performed using the factorial analysis of variance model, with replication (Zar 1974, p. 163-169). One factor was pond (or meadow), the other transect. The interaction term (pond/meadow x transect) was also defined. Since this is a random effects (Model II) analysis, multiple comparisons were not performed. Analyses were performed using the Data Desk® 3.0 exploratory analysis package.

3.5 Results

Full Beaver Ponds

(a) Variation in Soil Factors within Ponds

As only two samples were taken for soil factors within each transect, analyses were not performed to determine differences within individual ponds. In general, few of the ponds showed statistically significant variation in soil factors across transects. The Tukey box plots for each of the 6 ponds is in Appendix 1. Mean values for each pond are presented in Table 3.2. Summaries for each of the four soil factors are given below.

Soil Bulk Density

Bulk density values did not show a large amount of variation between transects for any of the six ponds. Mean values generally ranged between 0.2 and 0.95, with the highest values reached in ponds 1, 3 and 4 and lowest values in ponds 2, 6 and 7. No systematic trends in bulk density was seen across transects, although the highest values occurred at transect 2 (dam face) for four of the ponds (1, 2, 3 and 6).

Soil Organic Matter

Mean values ranged 10% to 55%, with the highest values in ponds 2, 4 and 6 and 7 and the lower values in ponds 1 and 3. In general, high bulk density values were associated with low organic matter values, and vice versa. Organic content was lowest in transect 2 in three of the ponds (1, 2, and 3). Pond 7 showed the opposite trend, with lowest organic content in transect 4. general organic matter content and bulk density are inversely

Table 3.2 Mean values for the soil factors as determined for the full ponds.

Pond No.	Conductivity (μs)	Transect No.					Mean
		1	2	3	4	5	
1		469	289	348	498		401
2		448	415	401	422	373	412
3		279	250	388	375		323
4		497	1030	388	583		624
6		366	299	562	427		413
7		782	983	836	724		831
Mean		473	544	487	505		

Pond No.	Bulk Density (g/ml)	Transect No.					Mean
		1	2	3	4	5	
1		0.69	0.94	0.71	0.53		0.72
2		0.32	0.68	0.26	0.33	0.49	0.41
3		0.49	0.92	0.52	0.37		0.58
4		0.27	0.40	0.95	0.75		0.59
6		0.38	0.50	0.26	0.33		0.37
7		0.21	0.20	0.21	0.28		0.23
Mean		0.39	0.61	0.48	0.43		

Pond No.	Organic Matter (%)	Transect No.					Mean
		1	2	3	4	5	
1		18.65	10.94	25.32	26.92		20.46
2		44.73	14.97	47.65	43.79	32.52	36.73
3		24.87	12.13	21.79	40.15		24.74
4		55.63	45.82	26.14	36.13		40.93
6		40.74	37.90	65.14	45.62		47.35
7		54.45	52.19	46.44	37.75		47.71
Mean		39.84	28.99	38.75	38.39		

Pond No.	pH	Transect No.					Mean
		1	2	3	4	5	
1		7.56	7.71	7.50	7.52		7.57
2		7.57	7.69	7.24	7.46	7.28	7.45
3		7.61	7.60	7.46	7.49		7.54
4		7.52	7.42	7.43	7.49		7.46
6		7.28	7.34	7.05	7.22		7.22
7		7.62	7.29	7.49	7.53		7.48
Mean		7.53	7.51	7.36	7.45		

correlated. Percent organic matter content ranged from 15 - 65%, and showed considerable variation within a given transect or a given meadow.

Soil Conductivity

Again, no noticeable differences were found between transects of a given pond. Mean values ranged between 250 and 1030 μs . The highest values occurred in ponds 4 and 7, with lower values in ponds 1, 2, 3 and 6. No clear trends with transect position were apparent for any of the ponds.

Soil pH

There were no statistically significant differences between transects for any of the ponds. Soils were slightly basic, with mean values ranging between 7.05 and 7.69. There was as much variation within ponds as between ponds. For most ponds, transects 1 and 2 (dam top and dam face) had slightly higher pH values than the other transects.

The results indicate that, while there is some variation in soil factors between transects within a given pond, these differences are not statistically significant. This indicates that soil conditions at a given pond site are similar.

(b) Variation in Soil Factors between Ponds

Separate two-way (factorial) analyses of variance were undertaken for each of the four soil factors. Each soil factor is described in turn.

Soil Bulk Density

No significant differences were found between transects or between ponds, and the interaction term was not significant (Table 3.3, Figure. 3.2). Ponds 2, 3, 6 and 7 have the somewhat lower median bulk density values (0.385 - 0.4), with the highest values occurring in ponds 3 (0.55) and pond 1 (0.75). There was little variation across transects.

Soil Organic Matter

Differences between ponds, and between transects, were not statistically significant (Table 3.3, Figure 3.3). Ponds 1, 2 and 3 have the lowest median organic contents (15 - 25%), and ponds 4, 6 and 7 the highest (40 - 50%). However, there was considerable variation within a pond so that these differences were not statistically significant.

Soil Conductivity

There was a statistically significant differences between ponds (Table 3.3, Figure 3.4). No trend across the transects was apparent. Pond 3 had the lowest median conductivity (300 μs), ponds 1, 2, 4 and 6 had intermediate values (400 - 500 μs), and pond 7 the highest value (850 μs). The interaction term was also significant in this analysis. This may be the result of the very high values on transect two in ponds four and seven.

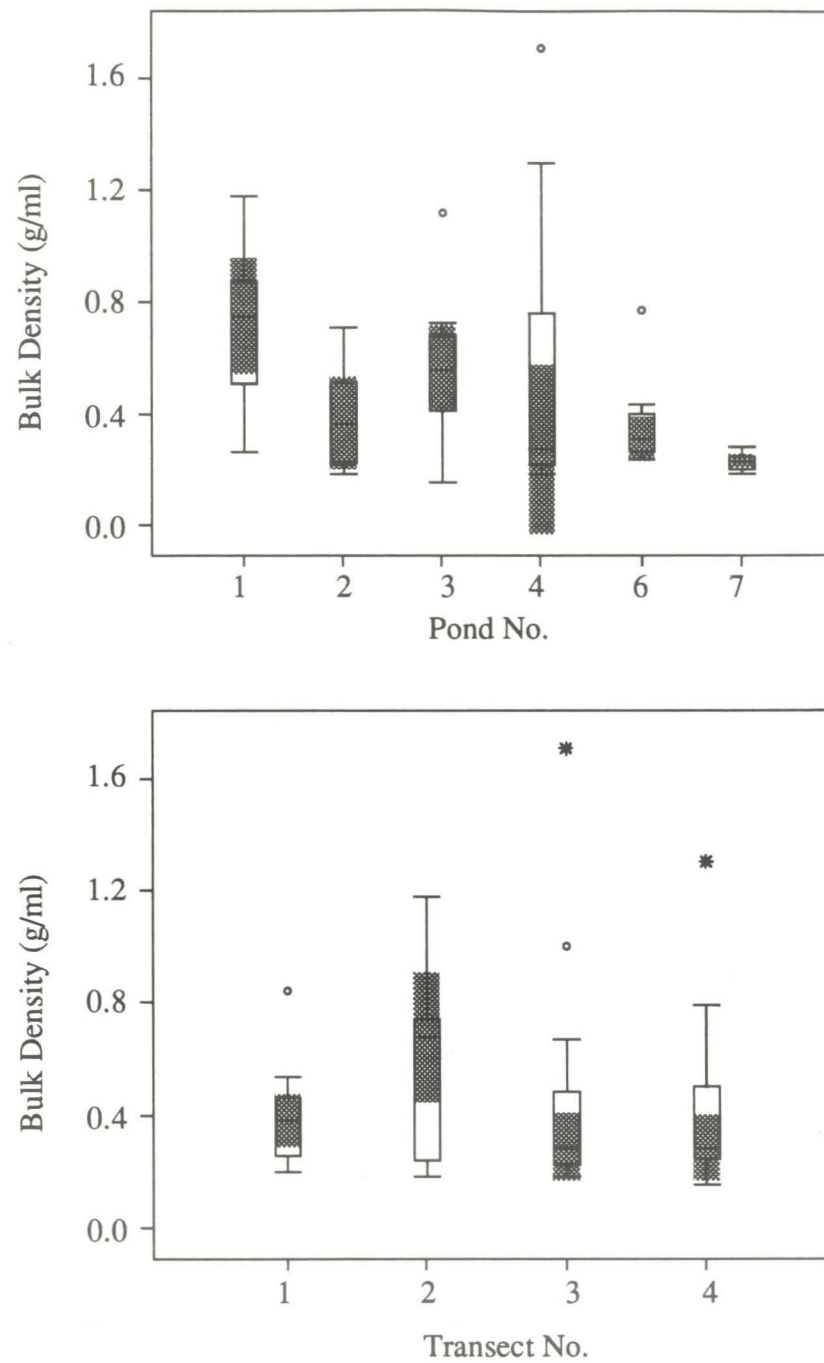


Figure 3.2 Box plots of bulk density (g/ml) in the individual ponds, and summarized by transect.

Table 3.3 Analysis of variance for soil factors in the ponds

Bulk Density (g/ml)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Pond (P)	5	1.292	0.258	2.251	0.082
Transect (T)	3	0.316	0.105	0.917	0.447
PxT	15	1.083	0.072	0.629	0.823
Error	24	2.756	0.115		
Total	47	5.447			

Organic Matter (%)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Pond (P)	5	5282.340	1056.470	2.023	0.111
Transect (T)	3	914.363	304.788	0.584	0.632
PxT	15	3819.760	254.650	0.488	0.924
Error	24	12532.000	522.167		
Total	47	22548.500			

Conductivity (μ s)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Pond (P)	5	1440362.000	288072.000	14.136	0.000
Transect (T)	3	33922.700	11307.600	0.555	0.650
PxT	15	680770.000	45384.700	2.227	0.039
Error	24	489100.000	20379.200		
Total	47	2644155.000			

pH					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Pond (P)	5	0.612	0.122	5.979	0.001
Transect (T)	3	0.204	0.068	3.323	0.037
PxT	15	0.336	0.022	1.095	0.409
Error	24	0.491	0.021		
Total	47	1.643			

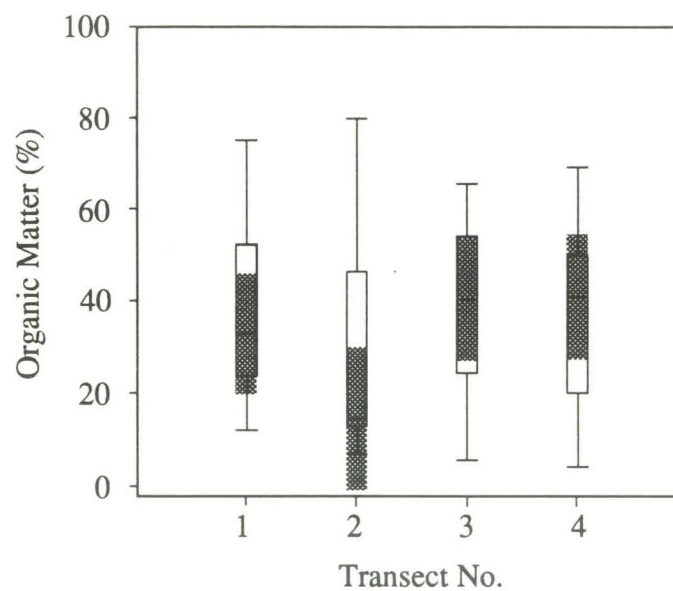
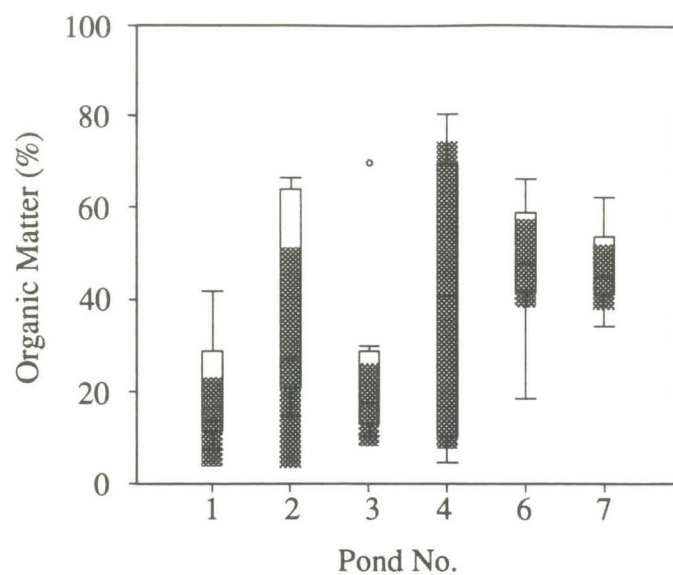


Figure 3.3 Box plots of organic matter (%) in the individual ponds, and summarized by transect.

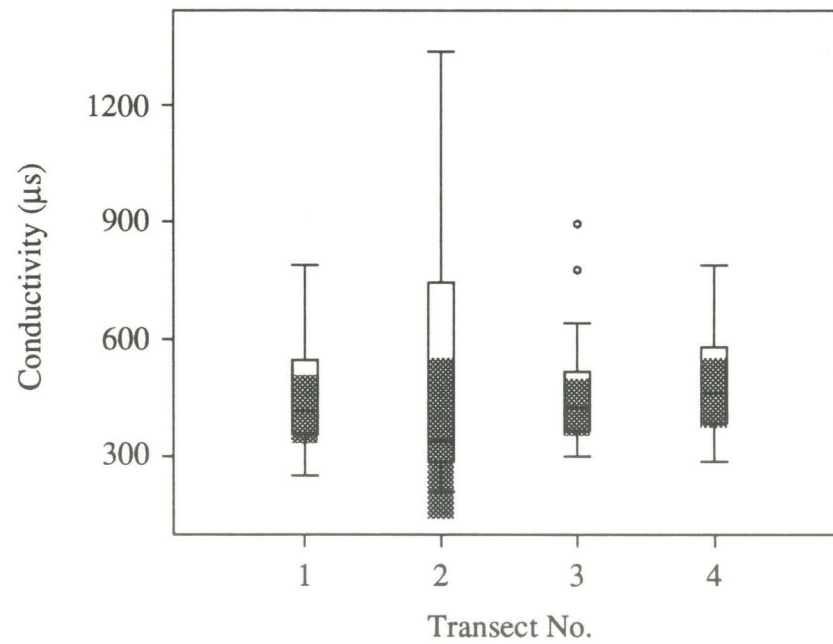
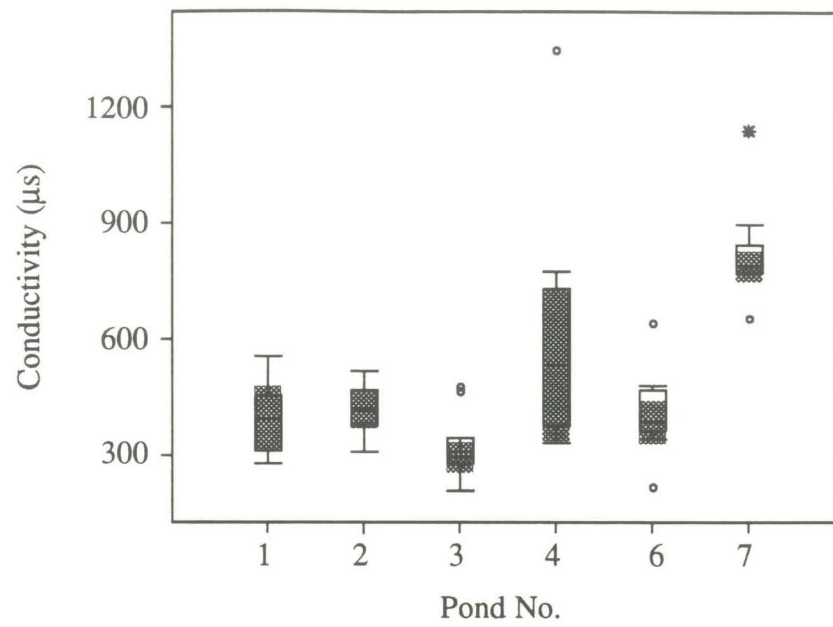


Figure 3.4 Box plots of conductivity (μs) in the individual ponds, and summarized by transect.

Soil pH

Once again, statistically significant differences were found (Table 3.3 Figure 3.5). A trend of decreasing soil pH from the dam top (transect 1) to the final transect (transect 5) was noted, and it was significant ($p = 0.037$). The differences between the ponds was also significant. Soil pH was lowest in pond 6 (median = 7.2), with the other five ponds having median pH values in the range 7.5 - 7.6.

Beaver Meadows

(a) Variation in Soil Factors within Beaver Meadows

In general, few of the meadows showed statistically significant variation in soil factors across transects. The ANOVA tables for each of the eleven meadows are presented in Table 3.4, and the Tukey box plots in Appendix 1. Mean values for each transect, and for each meadow, are presented in Table 3.5. Summaries of the variation for each of the four soil factors follow:

Soil Bulk Density

For six of the eleven meadows, statistically significant differences ($P < 0.06$) in soil bulk density across transects were present. In most cases, this reflected higher bulk density values on the dam top and dam face (transects 1 and 2) relative to the meadow transects 3 - 5. Median bulk density values ranged from 0.125 to 0.6

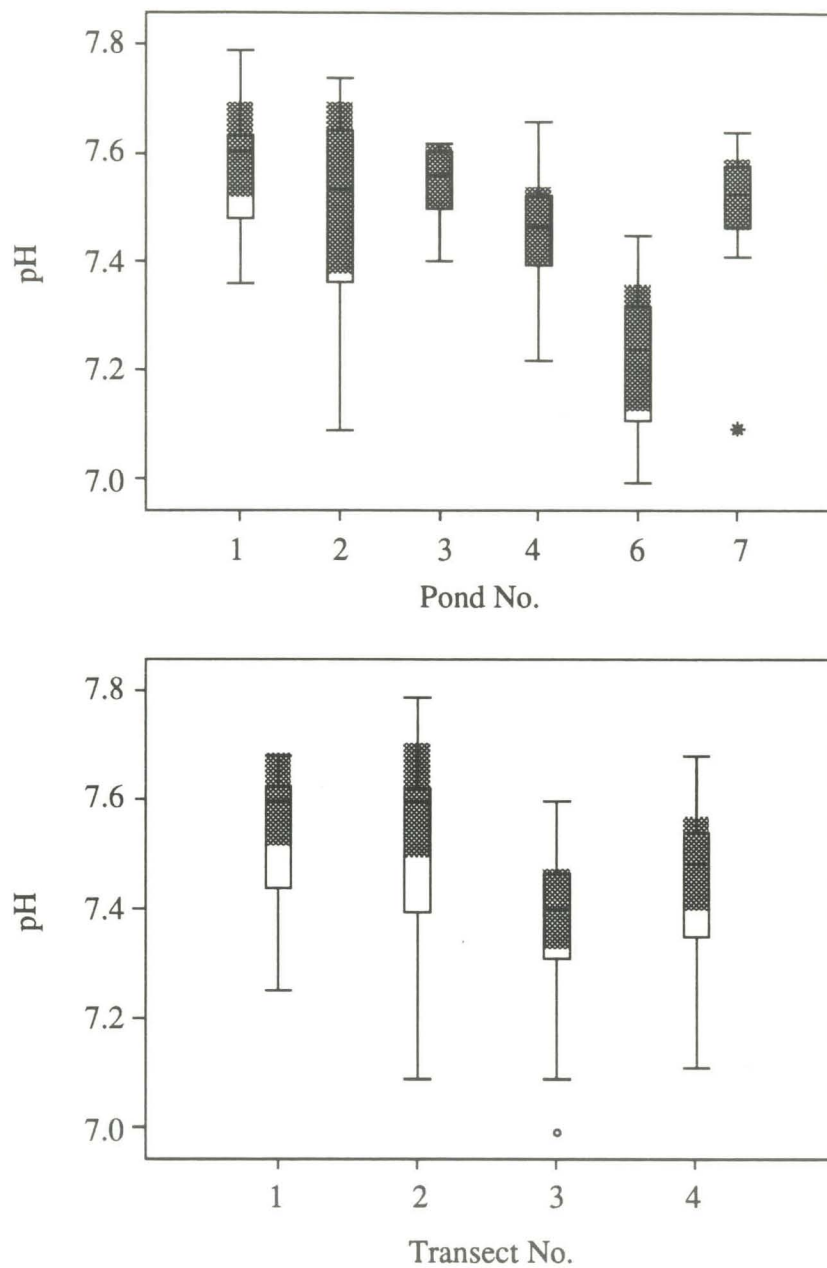


Figure 3.5 Box plots of pH in the individual ponds, and summarized by transect.

Table 3.4a Analysis of variance results for individual meadow soil factors.

Meadow No. 1 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	5.218	0.009
Organic Matter	0.709	0.599
Conductivity	2.740	0.071
pH	0.340	0.848
Soil Water	5.160	0.009

Meadow No. 2 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	4.379	0.019
Organic Matter	1.948	0.162
Conductivity	2.018	0.151
pH	0.270	0.892
Soil Water	8.191	0.002

Meadow No. 3 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	0.376	0.774
Organic Matter	0.546	0.672
Conductivity	0.765	0.554
pH	3.274	0.101
Soil Water	2.037	0.210

Meadow No. 5 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	0.246	0.862
Organic Matter	0.0534	0.983
Conductivity	0.189	0.901
pH	8.428	0.007
Soil Water	1.572	0.270

Table 3.4b Analysis of variance results for individual meadow soil factors.

Meadow No. 7 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	2.678	0.110
Organic Matter	1.074	0.408
Conductivity	2.761	0.104
pH	0.752	0.548
Soil Water	0.805	0.522

Meadow No. 8 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	3.181	0.050
Organic Matter	2.745	0.074
Conductivity	0.229	0.917
pH	0.238	0.884
Soil Water	1.187	0.362

Meadow No. 11 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	1.431	0.276
Organic Matter	3.919	0.034
Conductivity	0.725	0.554
pH	0.745	0.543
Soil Water	3.700	0.038

Meadow No. 12 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	3.561	0.060
Organic Matter	5.069	0.025
Conductivity	0.049	0.985
pH	6.633	0.012
Soil Water	21.450	0.001

Table 3.4c Analysis of variance results for individual meadow soil factors.

Meadow No. 14 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	3.994	0.052
Organic Matter	3.286	0.079
Conductivity	5.389	0.025
pH	1.663	0.251
Soil Water	2.478	0.136

Meadow No. 15 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	11.790	0.001
Organic Matter	7.965	0.004
Conductivity	0.210	0.887
pH	0.282	0.837
Soil Water	10.396	0.001

Pond No. 4 ANOVA of transects		
Soil Factor	F-ratio	Probability
Bulk Density	0.198	0.895
Organic Matter	0.105	0.955
Conductivity	0.350	0.775
pH	0.745	0.552
Soil Water	0.492	0.697

Table 3.5a Table of individual meadow organic matter means for whole meadows and by transect.

Organic Matter (%)		Transect No.					Mean
Meadow No.	Age (yrs)	1	2	3	4	5	
p4	1	53.20	49.02	43.60	49.37		48.80
3	6	34.30	35.77	44.06	42.90		39.26
11	6	19.40	23.94	44.64	42.56		32.63
12	6	42.50	28.83	59.07	48.63		44.76
15	6	30.30	28.33	54.27	57.21		42.53
1	9	24.30	40.94	38.63	48.09	44.70	37.99
2	9	35.40	25.79	40.77	47.76	41.51	37.43
7	9	26.50	43.42	50.20	36.61		39.18
14	9	44.80	16.19	51.32	32.66		36.24
5	21	36.70	33.95	32.69	38.16		35.37
8	22	53.90	27.03	46.47	49.50	35.53	44.23
Mean		36.48	32.11	45.97	44.86	40.58	

Table 3.5b Table of individual meadow water content means for whole meadows and by transect.

Water content (%)		Transect No.					Mean
Meadow No.	Age (yrs)	1	2	3	4	5	
p4	1	57.10	73.52	70.27	66.83		66.93
3	6	50.70	64.19	69.50	53.69		59.52
11	6	36.10	50.30	60.64	56.19		50.81
12	6	49.90	58.47	78.41	76.08		65.72
15	6	33.90	46.59	64.10	67.60		53.05
1	9	38.20	43.26	52.40	70.02	60.47	50.97
2	9	42.60	45.34	67.50	72.92	59.10	57.09
7	9	54.90	71.33	68.80	65.81		65.21
14	9	57.80	50.50	76.02	67.56		62.97
5	21	38.60	60.99	60.41	63.58		55.90
8	22	60.70	57.82	63.23	70.87	59.13	63.15
Mean		47.32	56.57	66.48	66.47	59.57	

Table 3.5c Table of individual meadow bulk density means for whole meadows and by transect.

Bulk Density (g/ml)		Transect No.					Mean
Meadow No.	Age (yrs)	1	2	3	4	5	
p4	1	0.23	0.16	0.21	0.17		0.19
3	6	0.35	0.28	0.23	0.34		0.30
11	6	0.42	0.28	0.27	0.33		0.32
12	6	0.22	0.28	0.17	0.15		0.20
15	6	0.40	0.51	0.15	0.11		0.29
1	9	0.43	0.57	0.37	0.22	0.22	0.40
2	9	0.29	0.45	0.25	0.19	0.26	0.29
7	9	0.40	0.25	0.14	0.21		0.25
14	9	0.21	0.43	0.15	0.33		0.28
5	21	0.35	0.45	0.39	0.28		0.37
8	22	0.33	0.43	0.23	0.14	0.36	0.28
Mean		0.33	0.37	0.23	0.22	0.28	

Table 3.5d Table of individual meadow conductivity means for whole meadows and by transect.

Conductivity (ms)		Transect No.					Mean
Meadow No.	Age (yrs)	1	2	3	4	5	
p4	1	950	2779	2826	1994		2137
3	6	1449	782	1296	935		1115
11	6	692	945	752	656		761
12	6	1100	1148	1084	1072		1101
15	6	1187	888	1014	1102		1048
1	9	967	421	1029	957	1428	844
2	9	1294	510	1242	932	1310	994
7	9	566	1410	1155	740		968
14	9	1353	547	1249	715		966
5	21	707	733	765	856		765
8	22	866	911	766	725	791	817
Mean		1012	1007	1198	971	1176	

.Soil Organic Matter

In general, organic matter of the soil increased from the dam top and face (transects 1 and 2) to the meadow itself (transects 3 - 5), though this trend was only statistically significant ($P < 0.05$) for meadows 11, 12 and 15 (also meadows 8 and 14 for $P < 0.1$). In

Table 3.5e Table of individual meadow pH means for whole meadows and by transect.

pH Meadow No.	Age (yrs)	Transect No.					Mean
		1	2	3	4	5	
p4	1	7.88	7.45	7.67	7.92		7.73
3	6	7.56	8.25	7.90	7.96		7.92
11	6	7.76	7.58	7.66	7.74		7.68
12	6	7.96	7.61	7.87	7.83		7.82
15	6	7.61	7.55	7.71	7.68		7.64
1	9	7.72	7.83	7.89	7.64	7.82	7.77
2	9	7.97	7.96	7.85	8.04	7.97	7.96
7	9	8.04	7.57	7.98	7.97		7.89
14	9	8.20	7.84	7.57	7.66		7.82
5	21	7.94	7.61	8.50	7.83		7.97
8	22	7.89	7.76	7.86	8.10	7.96	7.90
Mean		7.87	7.73	7.86	7.85	7.92	

general organic matter content and bulk density are inversely correlated. Percent organic matter content ranged from 15 - 65%, and showed considerable variation within a given transect or a given meadow.

Soil Conductivity

Conductivity values showed no systematic trend across transects, and showed statistically significant differences only for meadow 14 (transect 2, dam face, has lower value than the other transects). Mean values range between 761 μs (meadow 1) and 2137 μs (meadow p4).

Soil pH

Few trends in soil pH with transect position were seen for any of the eleven meadows. Two of the meadows (5 and 12) showed statistically significant differences in soil pH between transects. Mean values indicated basic soils in all cases (7.68 to 7.97)

Percent Water Content of Soil

In most of the meadows, an increase in the soil water content was observed from the dam top and face (transects 1 and 2) to the meadow transects (3 - 5). This trend was statistically significant ($P < 0.05$) for meadows 1, 2, 11, 12 and 15. Mean values ranged from 50 - 67%, and showed considerable variation between transects and between meadows.

(b) Variation in Soil Factors between Meadows

Separate two-way (factorial) analyses of variance were undertaken for each of the five soil factors (Table 3.6). Each soil factor is described in turn.

Soil Bulk Density

A significant differences were found between the eleven meadows. Values were significantly greater for transects 1 and 2 (dam top and face, median values of 0.33) than for meadow transects 3 and 5 (median values 0.2 to 0.22) (Table 3.6 and Figure 3.6).

Table 3.6 Analysis of variance for the soil factors in meadows.

Bulk Density (g/ml)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Meadow (M)	10	0.502	0.050	2.906	0.003
Transect (T)	3	0.589	0.196	11.346	0.000
MxT	30	0.777	0.026	1.498	0.069
Error	108	1.868	0.017		
Total	151	3.787			

Organic Matter (%)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Meadow (M)	10	3263.190	326.319	1.760	0.077
Transect (T)	3	6493.160	2164.390	11.670	0.000
MxT	30	6473.650	215.788	1.164	0.282
Error	105	19473.800	185.465		
Total	148	36468.600			

Conductivity (μ S)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Meadow (M)	10	19224664	1922466	5.741	0.000
Transect (T)	3	1042419	347473	1.038	0.379
MxT	30	12916893	430563	1.286	0.176
Error	108	36163768	334850		
Total	151	70746716			

pH					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Meadow (M)	10	1.764	0.176	1.692	0.092
Transect (T)	3	0.520	0.173	1.661	0.180
MxT	30	3.731	0.124	1.193	0.253
Error	108	11.260	0.104		
Total	151	17.196			

Soil Water (%)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Meadow (M)	10	5197.900	519.790	3.800	0.000
Transect (T)	3	9050.170	3016.720	22.053	0.000
MxT	30	5255.460	175.182	1.281	0.179
Error	108	14773.700	136.793		
Total	151	34880.800			

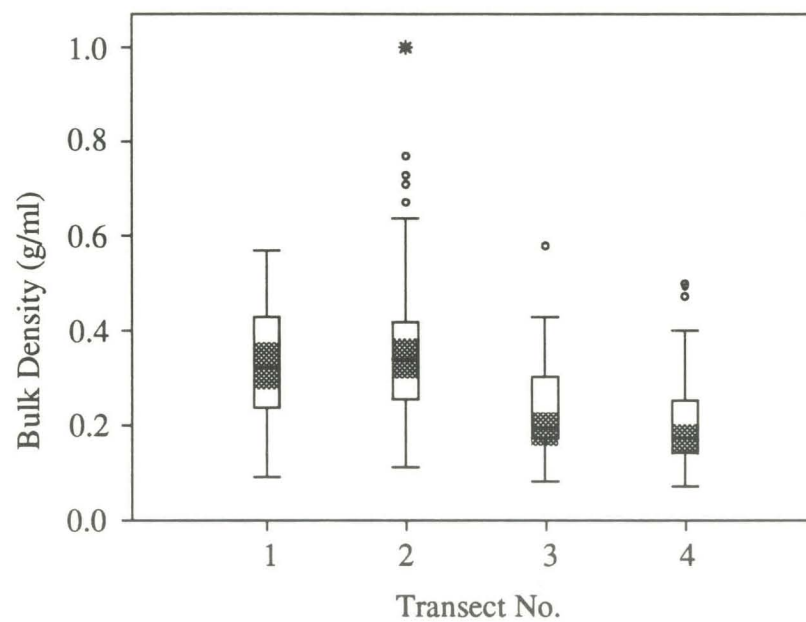
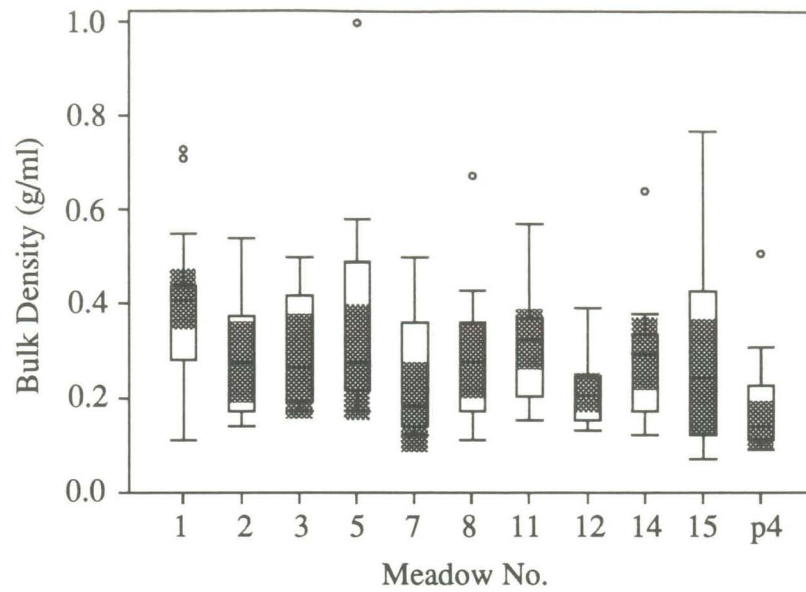


Figure 3.6 Bulk Density (g/ml) in the drained beaver ponds. The top figure is a box plot of the variation between the individual drained ponds while the bottom figure represents the transects of all individuals combined. For the results of the two factor ANOVA performed on this data see Table 3.6.;

Soil Organic Matter

No significant differences between the eleven meadows were observed, though the values for the one-year old meadow (p4) were somewhat higher than the others. Transect differences were seen, however, with transects 1 and 2 (dam top and face) having significantly lower median values (approximately 30%) than the meadow transects 3 - 5 (median values of approximately 50%)(Table 3.6 and Figure 3.7).

Soil Water

Significant differences were observed between the meadows as well as between the transects (Table 3.6 and Figure 3.8). The top of the dam and dam face were much drier than the rest of the meadow. The one year old meadow (p4) had the highest soil water values and there was considerable variation between meadows.

Soil Conductivity

A significant difference between meadows was observed, as the one year old meadow (p4) had a much higher median value (2000 μs) than the other meadows (less than 1250 μs) (Table 3.7 and Figure 3.9). Two of the soil cores from the one year old meadow were > 5000 μs .

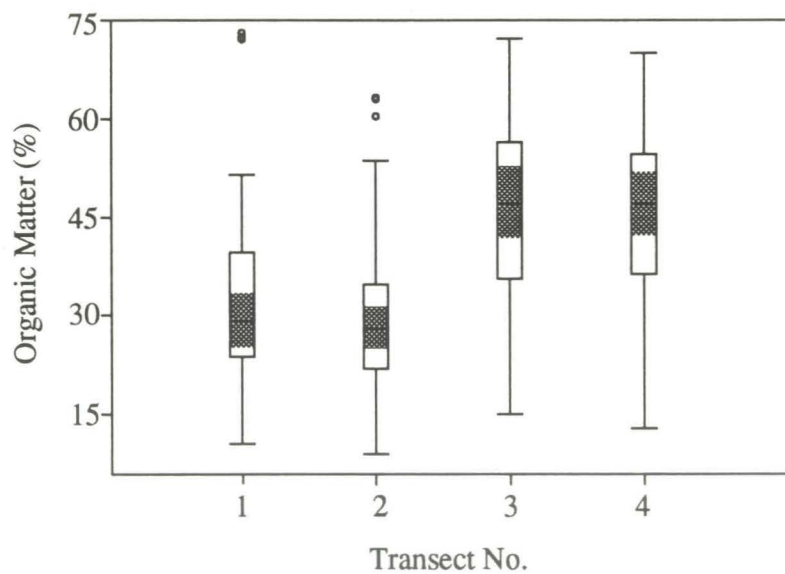
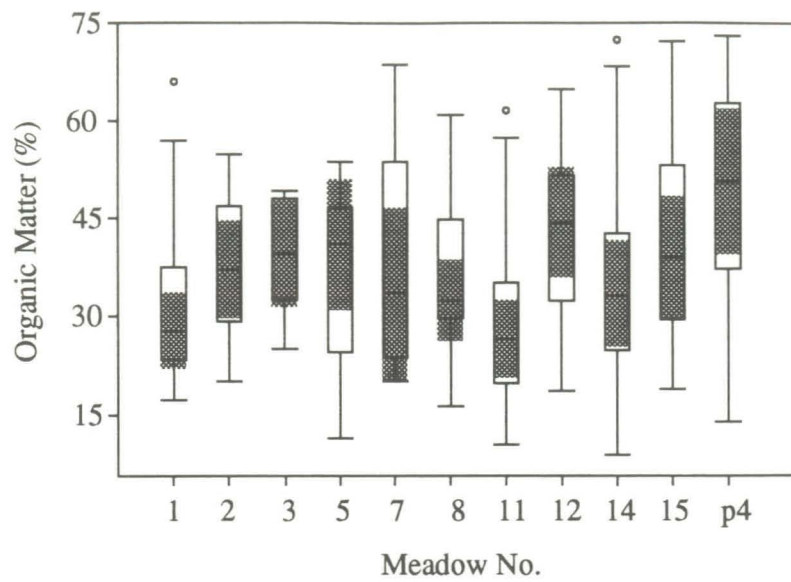


Figure 3.7 Percent organic matter in the drained beaver ponds. The top figure is a box plot of the variation between the individual drained ponds while the bottom figure represents the transects of all individuals combined. For the results of the two factor ANOVA performed on this data see Table 3.6.

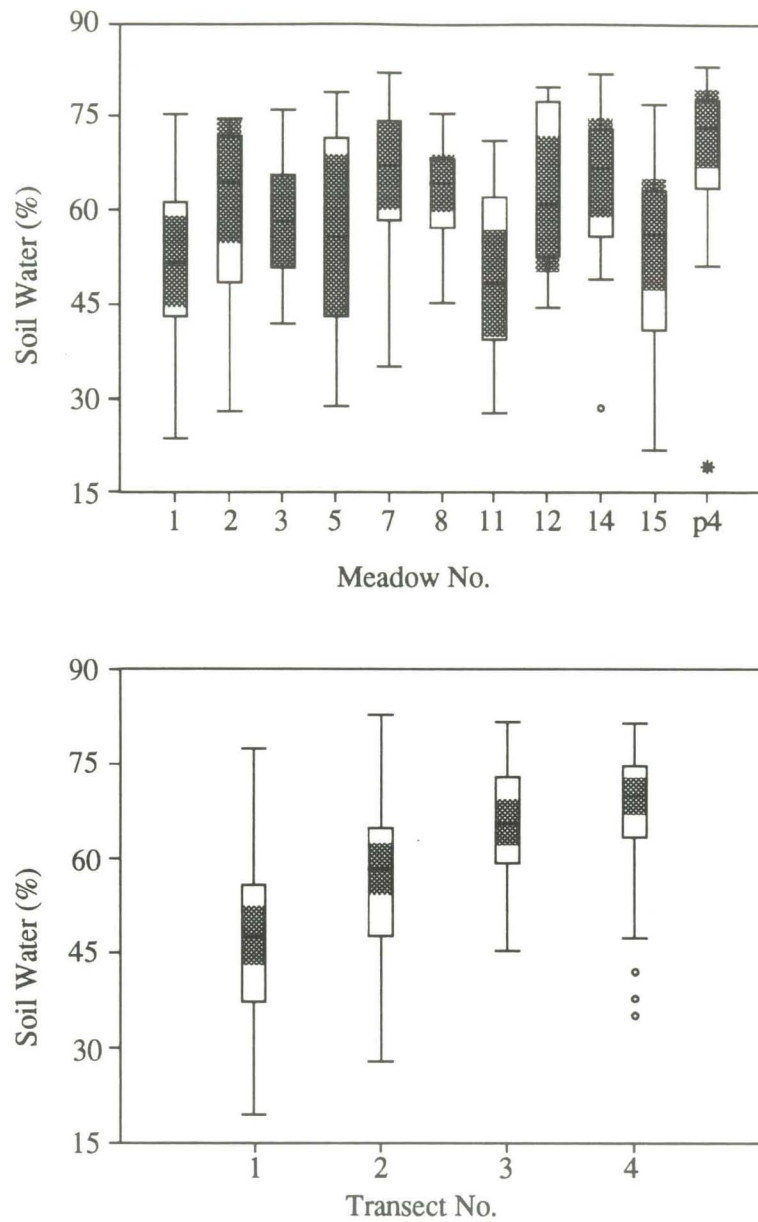


Figure 3.8 Percent soil water in the drained beaver ponds. The top figure is a box plot of the variation between the individual drained ponds while the bottom figure represents the transects of all individuals combined. For the results of the two factor ANOVA performed on this data see Table 3.6.

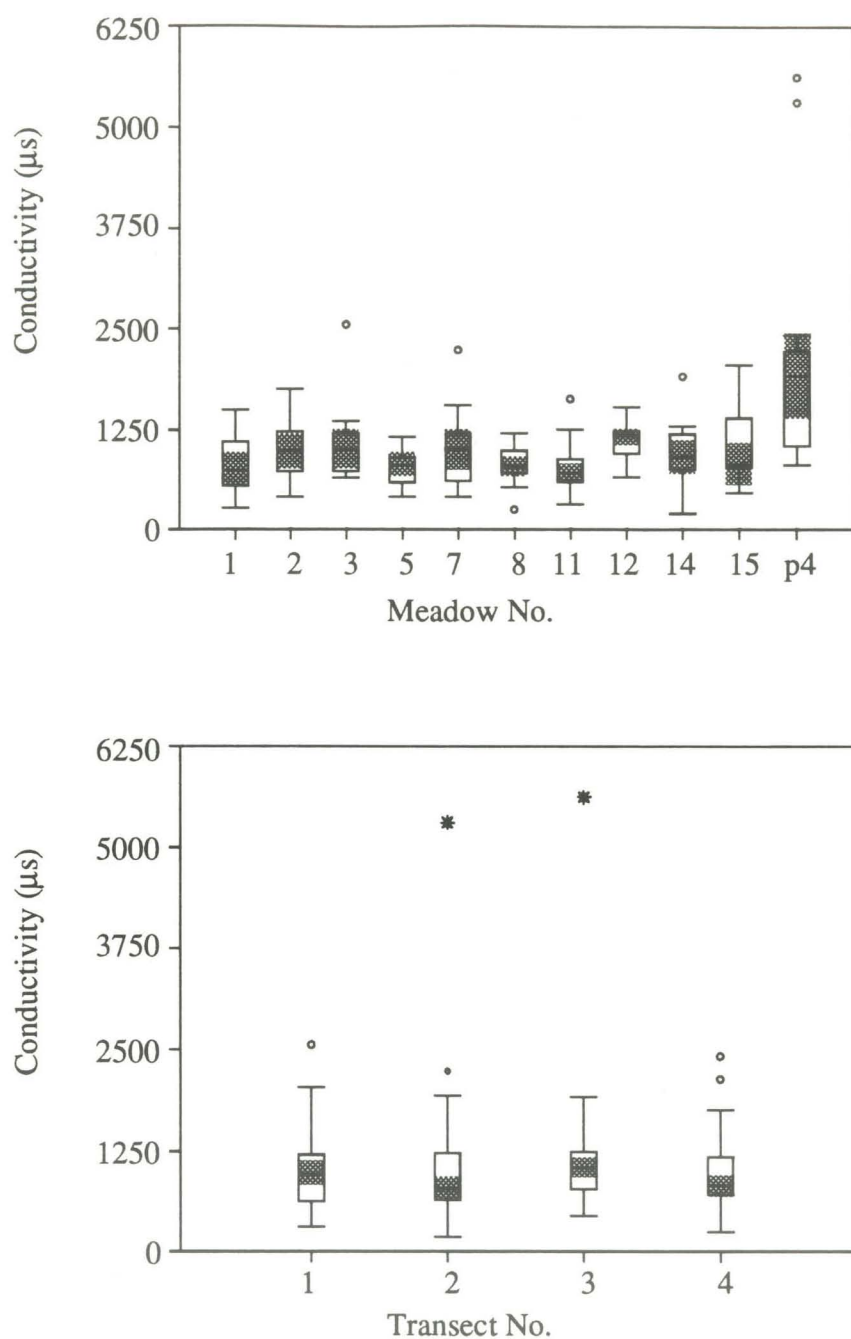


Figure 3.9 Conductivity (μs) in the drained beaver ponds. The top figure is a box plot of the variation between the individual drained ponds while the bottom figure represents the transects of all individuals combined. For the results of the two factor ANOVA performed on this data see Table 3.7.

Soil pH

No significant differences in soil pH across meadows or transects were observed (Table 3.6 and Figure 3.10). Values for transects ranged between 7.5 and 8.0. Meadows 11, 14 and p4 have the lowest median pH values (7.7), and meadows 2, 3, 4, 5 and 12 the highest (7.9).

(c) Variation in Soil Factors with Meadow Age

Statistically significant ($P < 0.1$) differences in soil factors with meadow age were found for most of the soil factors (Table 3.7 and Figure 3.11). The one year old meadow (p4) had higher soil conductivity, soil water content and organic matter and lower bulk density, than the older meadows. However, because only a single year-old meadow was sampled, it is difficult to determine whether these differences represent a consistent age trend or are specific to the particular meadow sampled.

3.6 Discussion

Soil Differences Within Ponds

All the ponds showed similar values for the four soil factors measured, despite differences in both their size and presumable 'age'. This is perhaps not surprising given that they are all filled with water, and that they occur in the same 'soil region' and along the same waterway. Any differences in soil factors that are observed in older meadows are therefore likely the result of biological and physical process that occur after the pond has

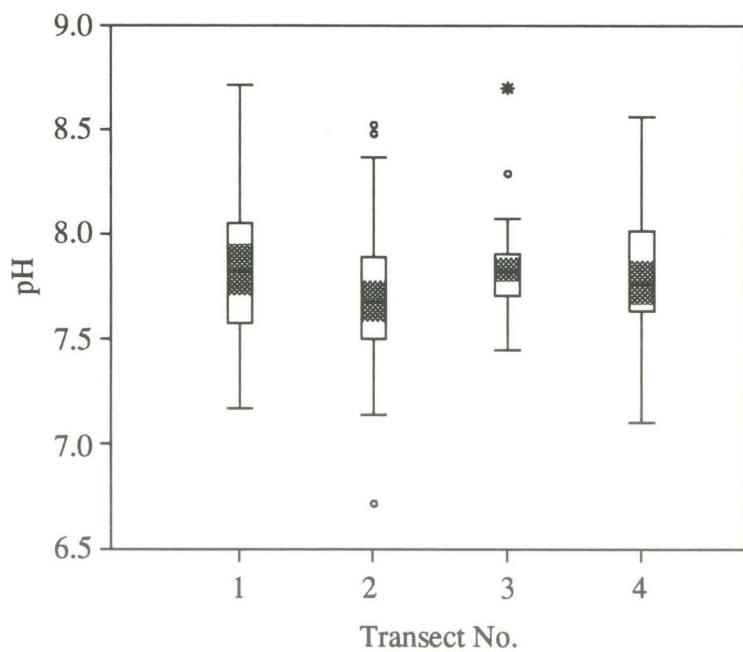
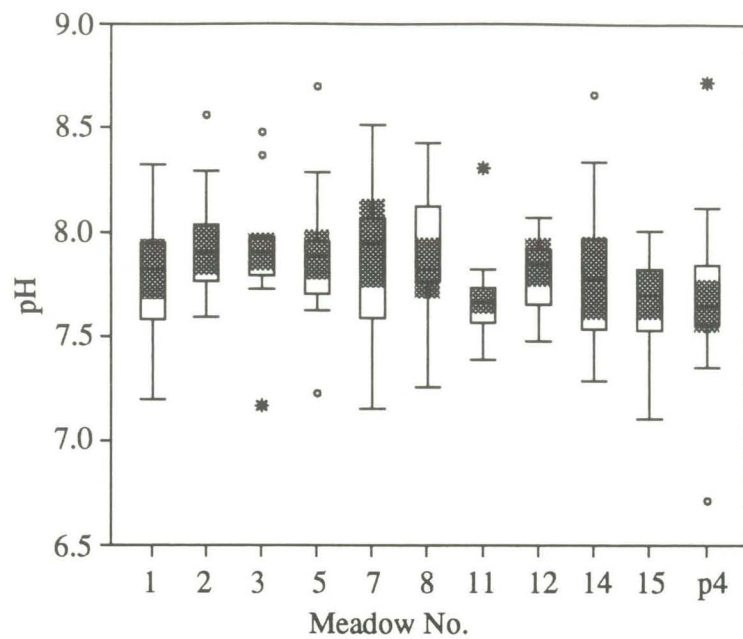


Figure 3.10 pH in the drained beaver ponds. The top figure is a box plot of the variation between the individual drained ponds while the bottom figure represents the transects of all individuals combined. For the results of the two factor ANOVA performed on this data see Table 3.6.

Table 3.7 Analysis of variance results for soil factors by meadow age

Bulk Density (g/ml)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Age	3	0.176	0.059	2.524	0.060
Error	147	3.417	0.023		
Total	150	3.593			

Organic Matter (%)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Age	3	1616.690	538.896	2.242	0.086
Error	145	34851.900	240.358		
Total	148	36468.600			

Conductivity (μ s)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Age	3	19167674	6389225	18.421	0.000
Error	147	50985648	346841		
Total	150	70153321			

pH					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Age	3	0.702	0.234	2.088	0.104
Error	147	16.474	0.112		
Total	150	17.177			

Soil Water (%)					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Age	3	1586.790	528.931	2.376	0.072
Error	147	32727.700	222.638		
Total	150	34314.500			

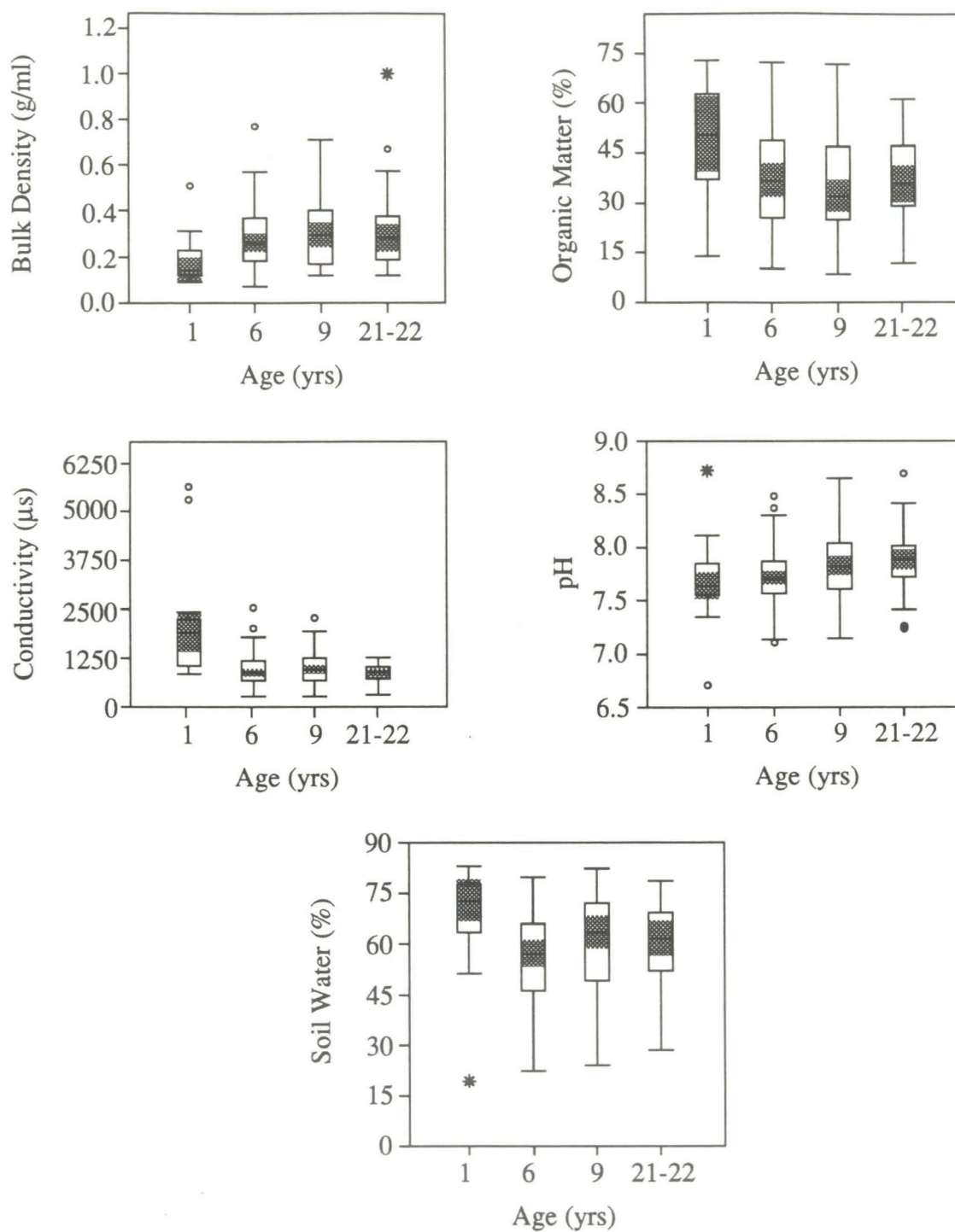


Figure 3.11 Box plots of variation in the five soil factors between the four different age categories.

drained and terrestrial vegetation has established. It is interesting to note that the soil chemistry of the one year old meadow (meadow p4) is more similar to the ponds than to the other meadows. This suggests that some changes in soil chemistry occur once the pond has drained. This is perhaps not surprising given the very different hydrological conditions prevailing prior to and following pond drainage.

Soil Differences within Meadows

The factorial analysis of variance results indicate that there are some differences in soil factors between the meadow transects. These differences are likely attributable to beaver activity during the process of dam building, and to changes in the hydrology of the system that occurs as the result of dam building (Naiman & Melillo 1984). A beaver dam is composed of sediment from the bottom of the traversed stream together with woody debris that has been removed from the streambank (Naiman & Melillo 1984, Naiman et al. 1986, Smith et al. 1989). New beaver dams are often built on top of old ones, so that some of the organic material contained in a dam may be highly decomposed. Within RMNP beaver were present and constructing dams prior to their local extirpation due to overhunting in the late 1800's (RMNP 1979). The possibility exists that portions of dams from that period were used by the beaver population that was reintroduced into the park in the 1940's. If this is the case, some dams may have portions that are quite old and whose original organic construction material is no longer determinable (M. Shaw, personal observation). This may be particularly true for areas near the streambank, where older material is less likely to have been washed away. Soils from transects 1 and 2 (dam top and dam face transects) will likely be most affected by this factor. If beaver use inorganic streambed material during dam construction and maintenance, dam top and dam face soils might be expected to have a higher bulk density and lower organic matter content than adjacent meadow areas (transects 3 - 5). If however beaver use material from the shallow

sides of the ponds where the emergent vegetation is present and organic content of the soil is higher, then the dam top and face would have soils of low bulk density and high organic content.

My results suggest that beaver use the more inorganic stream bed sediments in dam building, since the dam top and face soils have higher bulk density and lower organic matter content than the meadow transects 3 - 5. It was observed that main meadow areas have vegetation growing on it at all times, even when a beaver dam is present. This emergent vegetation (primarily grasses and sedges) continually adds organic matter to the soil. This, together with low levels of dissolved oxygen and the resulting slow rate of decomposition in ponds, may further increase the amount of organic matter deposited in the sediment (Smith et al. 1991). Naiman et al (1986) found that a full beaver pond serves to contain sediment that has flowed into the pond from upstream. This may further increase the amount of organic matter found in ponds (and eventually meadow) sediment. All these factors likely account for the high organic content of soil cores taken from meadow transects 3 - 5. Indeed, the meadow transects averaged > 50% organic matter, while the mean for the dam top and face was < 30%.

The observed inverse relationship between soil organic matter and bulk density reflects the higher total pore space of soils having higher organic content (Brady 1984). The higher pore space of more organic soils may account for the higher soil moisture levels in the main meadow relative to the dam top and face. The fact that the dam top is elevated above the surrounding meadow, and therefore more subject to gravitational drainage, may also reduce soil water content. Higher bulk density and lower moisture and organic content of soils from the dam top and face may result in some differences in the vegetation found there.

Meadow soil were slightly to moderately basic, suggesting that certain macronutrients (e.g., calcium, magnesium, phosphorus) and micronutrients (e.g., iron manganese, zinc cobalt and copper) may be difficult for plants to sequester.

Soil Differences between Meadows

There were few statistically significant differences between the eleven meadows for any of the five soil factors measured. This suggests that the underlying superficial soil parent material and soil processes are similar at all sites.

Age Differences

The results suggest that the soil factors of the one-year-old site (meadow p4) are somewhat different from those of the other ten, older meadows. This meadow has the highest conductivity (median of 2000 μs vs. 600-1200 μs), soil water (median of 73% vs. 48-70%) and organic matter content (median of 52% vs. 35-40%), and the lowest bulk density (median of 0.15 vs. 0.25 - 0.3) and pH (median of 7.6 vs. 7.7 - 7.9). These results suggest that the soil of newly drained ponds is more similar to a full pond than to an established wet meadow. The soil cores from meadow p4 were taken less than 4 months after the pond had drained, which might account for the higher soil moisture content. Changes in soil factors might be expected when the formerly waterlogged and oxygen-poor soil is exposed to the air, and as hydrological conditions change from a slow-moving standing water to a flowing stream. Unfortunately, only a single one year old meadow was sampled in the course of this study, so that it is impossible to determine whether the differences in soil factors observed truly reflects changes in soil chemistry following pond drainage.

3.7 Summary

1. There are few systematic trends in soil factors (between transects) within a given beaver pond, for the four factors measured (soil bulk density, organic content, conductivity and pH).
2. Few statistically significant differences in soil bulk density, organic content, conductivity and pH were found between the six beaver ponds sampled.
3. Within about half of the eleven meadows, statistically greater values for soil bulk density and water content, and lower values for soil organic matter, were observed for transects 1 and 2 (dam top and face) compared to meadow transects 3 - 5. No trends in soil conductivity and pH were observed, however. These results suggest that the soil of the dam top and face have higher inorganic content, and are better drained, than the wet meadow areas.
4. There were few significant differences in soil bulk density, organic matter, conductivity, pH and water content between the eleven meadows.
5. Soil conductivity and water content of the one year old meadow were significantly greater than values for the older meadows.
6. Soils in the beaver meadows and ponds are slightly to moderately basic and have relatively high organic content (20 - 50%). Bulk density values are generally in the range 0.2 - 0.6, and conductivity values in the range 500 - 1200 μ s.

Chapter 4 Seed Bank Dynamics of Beaver Ponds and Meadows

4.1 Introduction

The soil seed bank often plays an important role in site revegetation, particularly in regions undergoing periodic disturbances that remove the extant vegetation (van der Valk & Pederson 1989). Examples include the cyclic patterns of dynamic plant community change in prairie marshes (van der Valk and Davis 1979, van der Valk & Leck 1989), and vegetation change in alpine meadows (McGraw & Vavrek 1989). Studies have also been undertaken to examine the role that the seed bank, in combination with fire, plays in the vegetation dynamics of coniferous forest (Archibold 1989) and California chaparral ecosystems (Parker & Kelly 1989). Similar processes have been inferred for a number of other plant communities, but in many cases detailed studies are lacking (van der Valk & Pederson 1989). No studies have focussed on the role of the seed bank in the vegetation dynamics of beaver meadows following dam breaching and the exposure of mudflats.

The seed banks of wetlands have been extensively studied, and according to Leck (1989) most major wetland systems (with the notable exception of tropical forest wetlands, Garwood 1989) have had their seed bank surveyed. Such surveys have generally quantified seed bank composition by observations of germination from soil samples. Keddy & Reznicek (1982, 1986) have discussed the role of soil seed banks in perpetuating wet meadow vegetation along lakeshores. High lake water levels kill woody species and intolerant emergents. Once water levels fall, the exposed mudflats are colonized by species from the seed bank. Fluctuating water levels perpetuate this cycle. However, the authors recognized that large and frequent water level fluctuations will largely eliminate this shoreline vegetation, while the stabilization of lake levels will result in the dominance of

woody vegetation and emergent macrophytes (e.g., *Typha* sp.) along the shoreline. Similar processes appear to operate in North American prairie marshes that undergo natural decreases in water levels or 'drawdowns' (Walker 1959, 1965; van der Valk & Davis 1976, 1978; Pederson 1981; Poiani & Johnson 1989). The mudflats exposed during a drawdown are colonized from the seed bank by a number of annuals and emergent plant species. The artificial manipulation of water levels may be an important management strategy in such wetlands (Pederson & van der Valk 1984).

The beaver meadow complex (Naiman et al. 1988) is another example of a community that undergoes changes in water levels. Dam construction by beavers is a disturbance that results in the death of emergent plant species, and results in the invasion of the pond by aquatic vegetation. Dam breaching reverses this trend, with the exposed mudflat being colonized by terrestrial vegetation, either from the seed bank or through vegetative propagation. The exposed mudflat is thought to undergo an initial change from a wet-sedge meadow to one dominated by dry grasses and woody species (Naiman et al. 1988; Graham 1963).

The plant species that initially establish on mudflats may be derived from the seed bank, or result from the growth of vegetative propagules (e.g., rhizomes, root suckers) that have survived flooding. An examination of the soil seed bank, and an assessment of the relationship between the seed bank and the extant flora, can help determine which of these two factors is more important. If mudflats are recolonized by vegetative propagules that existed prior to the flooding, we would not expect a close correspondence between the soil seed bank and the extant vegetation, and might expect few changes in the extant vegetation over time. If however the seed bank is not appreciably different from the extant vegetation, then there is evidence that the exposed mudflat is initially colonized by species derived from the seed bank.

There may also be differences in the degree of similarity between the seed bank and the extant vegetation as a meadow ages. If the extant vegetation produces a large seed rain, and if the seed falls in the area immediately surrounding the parent plant, then a close correspondence between the seed bank and the extant vegetation is expected, and this correspondence would be expected to change little over time. If however the vegetation that establishes in these systems propagates by vegetative means, such that the constituent species are able to out compete the species that initially colonize the mudflat, then it would be expected that the seed bank and the vegetation would become less and less similar over time.

The seed banks of beaver ponds and meadows are derived either from seed produced by species growing in or around the pond, or from flotation from upstream sources. As river flow is by definition one-way, it might be expected that the seed banks of adjacent ponds or meadows might be more similar than those that are more spatially separated. This contrasts with previously-studied freshwater wetlands (lakeshores and prairie marshes) in which a one-way flow of water does not occur. In this respect riverine systems might be expected to differ in their seed bank dynamics.

The objectives of this study are:

- (1) to determine if there are changes in the soil seed bank over time (i.e. with increasing meadow age).
- (2) to compare and contrast the seed banks of full ponds and beaver meadows.
- (3) to determine the effect of a cold treatment on seed bank germination.

4.2 Materials and Methods

Full Ponds

Full ponds were selected using aerial photographs and ground truthing in the spring of 1991. All selected ponds were filled with water when sampled during the spring freshet of the first week of May, 1991. Since water levels were at their high point, I assumed that non-maintained dams would have been breached. Therefore the ponds sampled were assumed to be the result of active beaver dams. A total of six full ponds were sampled along the Little Saskatchewan River between Whitewater Lake and Lake Audy in RMNP (Figure 4.1).

Sampling

A minimum of 4 sampling transects were established at each pond. The first was along the top of the dam, at the spring water level. The second transect occurred along the base of the upstream face of the dam. A third transect was located 10 m upstream and parallel to the second transect. The fourth and fifth transects were located at further 10 m intervals, again parallel to the other transects. Seed bank sample cores were taken at 5 m intervals along each transect using a soil corer. Except for the dam top, the water depth of the sampling locations precluded the use of a traditional soil corer. A telescoping 4 m length of PVC pipe, 4 cm inside diameter, was used to take soil cores from the ponds. Depending on pond size and depth, and current strength, cores from the center of the pond were taken with the help of either chest waders or a small rubber raft. At one site cores from the south shore were not taken since the substrate was still frozen.

For all soil cores, the top 10 cm of the substrate were removed and immediately placed in sealed and labelled plastic bags. These bags were kept in a cooler until they could be transported to a cold room at the University of Manitoba, Department of Botany. A total of 256 soil cores were taken from the six ponds (Table 4.1).

Greenhouse Growth and Species Determination

Because the soil cores were taken in the early spring, they were not subjected to a cold treatment prior to germination. Germination trials to determine seed bank composition were performed. A 35 ml random subsample was taken from each soil core and mixed with 400 ml of water. This mixture was homogenized, and then poured into 15 cm diameter pots filled with a sterilized soil mixture of 2 parts greenhouse soil, 1 part silica sand, and 1 part commercial Sphagnum peat. A total of 270 pots were used, including 14 in which no field samples were added. These served as 'controls' to ensure that no residual seed survived the soil sterilization procedure.

On May 22, 1991 the pots were randomly positioned on a bench in the south glasshouse of the Department of Botany roof top greenhouse (temperature range of 15-25°C). Pots were watered as necessary (daily in sunny weather, every second day during cloudy periods). Emerging seedlings were allowed to grow until they were identifiable to species, at which time they were recorded and then carefully removed from the pot. Once a pot contained no species, it was left on the bench for an additional 21 days, after which it was assumed that no other viable seeds were present. A few of the sedges were impossible to identify to species as they did not flower over the duration of the experiment. In such cases plants were identified to genus and separately recorded (e.g., species A, B, C etc.).

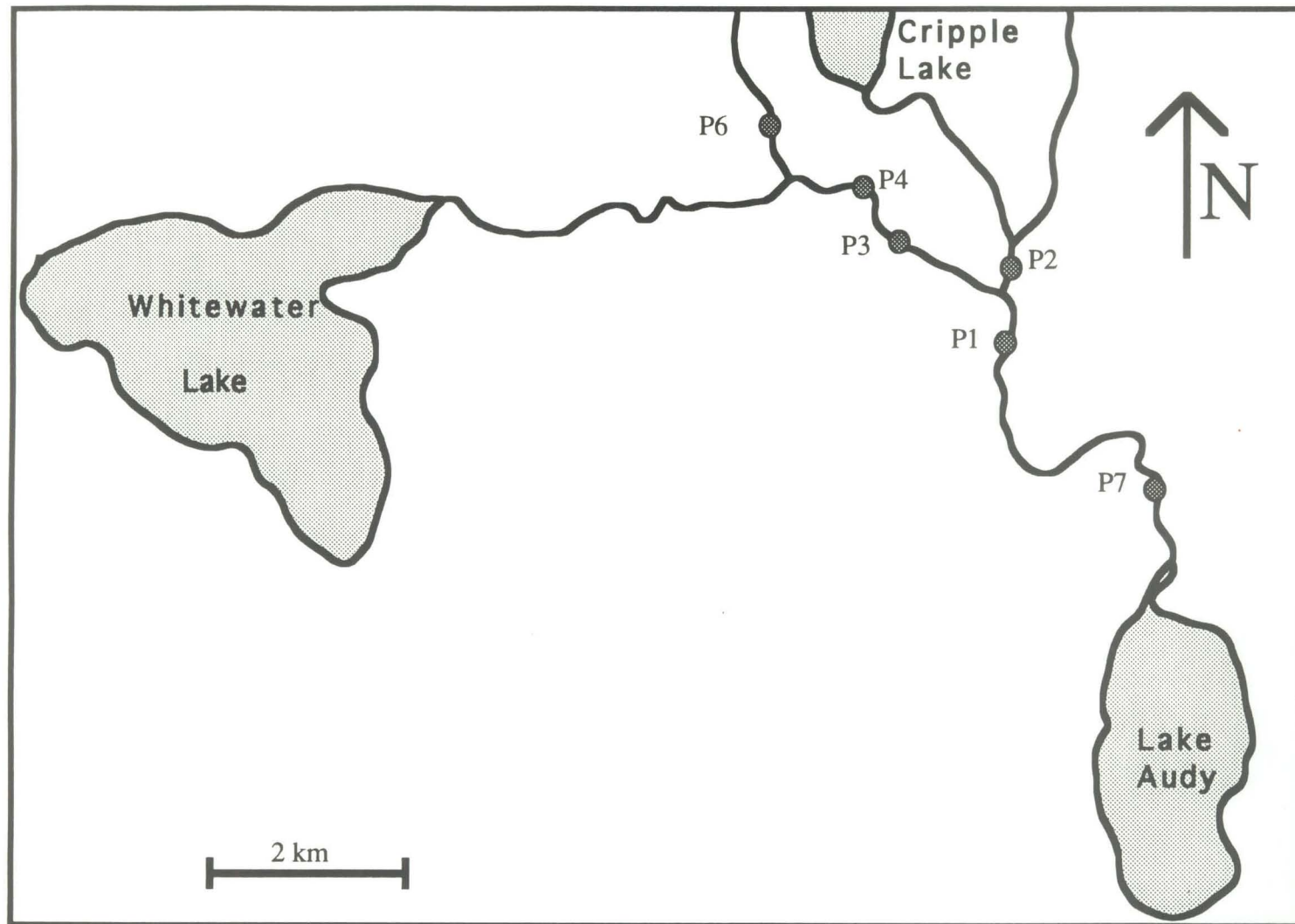


Figure 4.1 Little Saskatchewan River from Lake Audy to Whitewater Lake. All ponds that were sampled are shown.

Table 4.1 Number of samples and species found in the seed banks of the full ponds and the drained ponds. In the drained ponds (meadows) a total of 77 different species of vascular plants were recorded.

Full ponds

Pond No.	No. Transects	No. Samples	No. species
1	4	32	21
2	5	54	26
3	4	42	25
4	4	29	24
6	4	39	31
7	4	53	27
Total	25	249	44

Cold Treated Meadow

Meadow No.	Meadow age	No. transects	No.samples	No. species
p4	1	4	18	18
3	6	4	18	14
11	6	4	15	20
12	6	4	19	24
15	6	4	12	21
1	9	5	12	25
2	9	5	12	21
7	9	4	19	14
14	9	4	10	19
5	21	4	12	13
8	22	5	13	23
Total		47	160	55

Non-Cold Treated Meadow

Meadow No.	Meadow age	No. transects	No.samples	No. species
p4	1	4	18	18
3	6	4	18	13
11	6	4	15	21
12	6	4	19	18
15	6	4	12	16
1	9	5	12	20
2	9	5	12	17
7	9	4	19	12
14	9	4	10	16
5	21	4	12	21
8	22	5	13	23
Total		47	160	44

Beaver Meadows

The soil seed banks of beaver meadows were sampled during the vegetation survey, in the last two weeks of August, 1991. Eleven meadows over five age categories (1, 6, 9, 21, 22 years) were sampled. The single one-year-old meadow was also sampled as a pond in the spring of 1991.

Sampling

The sampling procedure was similar to that used for the ponds, with transects positioned along the dam top (transect 1) and dam face (transect 2). However, the third through fifth transects were positioned 20 m, as opposed to every 10 m, apart. Soil cores were taken from every second quadrat enumerated in the vegetation survey (every 5 or 10 m along each transect, depending on transect length). A small hand-held 5 cm diameter soil corer was used to remove the top 10 cm of soil. Each core was placed in a labelled bag and kept in a cooler until transported to a cold room at the University of Manitoba, Department of Botany. A total of 160 soil cores were taken (Table 4.1).

Greenhouse Growth and Species Determination

Because the beaver meadow seed bank cores were taken in August, and because it is known that many seeds of temperate plant species require a vernalization treatment (Baskin & Baskin 1989), it was decided to divide each soil core into two halves or 'treatments'. The first was subjected to no cold treatment (i.e. the soil seed bank was germinated immediately), while the second was subjected to cold treatment prior to the germination trials. Cold treatment was accomplished by placing bagged soils in a commercial freezer

(kept at -14°C) for two months, followed by an additional three weeks in a cold room at 4°C . This allowed the soil to slowly thaw and simulated conditions in the early spring. Germination trials and species identification methods were identical to those used for the pond soil cores.

Data Analysis

Trends in species richness

For the pond seed banks, the number of individuals of each species was recorded for each of the 249 soil cores. The data were then summarized by computing the number of species per pot (i.e. 'species richness' per 35 ml of soil). Species richness was computed for soil volume rather than total species richness since sample sizes of the ponds and meadows differed. For the beaver meadow seed banks, the number of individuals of each species was determined by adding the values obtained for the non-cold and cold treatments. This was done as this is the best true estimate of the seed bank present. As for the pond data, the number of species per pot, per transect, and per meadow was computed. Analyses were also undertaken to determine whether the seed bank of the non-cold and cold treatments were statistically different.

One-way analyses of variance (ANOVA; Zar 1974, p. 133-139) was performed to: (a) determine if species richness, per soil core, varied with meadow age; (b) determine if there are differences in species richness between the cold-treated and non cold-treated meadow soil cores; (c) determine if there are differences between meadow and pond soil cores. Since this is a random effects model, multiple comparisons were not performed. Analyses were performed using the Data Desk[®] exploratory analysis package.

For both the pond and meadow seed banks, two way (factorial) analysis of variance with interaction (Zar 1974. p. 163-169) was performed to detect differences in seed bank species richness between transects and ponds/meadows. Since this is a random effects model, multiple comparisons were not performed. Analyses were performed using the Data Desk® exploratory analysis package.

Correspondence analysis

Correspondence analysis (CA; Benzécri 1991) ordination was performed to examine trends in the seed bank of the ponds and meadows. This method, which is also known as reciprocal averaging (Hill 1973), is an eigenvector method of ordination related to principal components analysis (Kenkel & Orlóci 1986). The data structure is treated as a contingency table, and successive linearly uncorrelated ordination axes are extracted which maximize the canonical correlation between the scores of the variables (e.g., species) and individuals (e.g., quadrats, or sites). The method results in a biplot of the variables and individuals in an ordination diagram.

The following data sets were examined using this ordination method:

- for each of the six ponds, the frequency of occurrence of each species along each transect was computed. This gave a species (= 44 for the ponds) by site (= 25 transects) that was ordinated to examine differences between pond seed banks and variation between transects.
- for each of the eleven meadows, the frequency of occurrence of each species along each transect was determined. This gave a species (= 75 for the meadows) by site (= 47 transects), and this was ordinated to examine differences between the meadow seed banks as well as variation between transects.

- frequency of occurrence of species in each of the eleven meadows was determined (giving a 75 species x 11 meadow matrix). This was ordinated to determine if the seed bank in the meadows varied with meadow age.

Comparison of seed bank composition of ponds and meadows

A total of 77 species was recorded in the seed bank study. Differences in the abundances of common species between the ponds and meadows were examined by computing mean frequencies. An overall assessment of floristic difference between the seed banks of ponds and meadows was accomplished by first performing a correspondence analysis (CA) ordination on a species (= 77) by soil core (= 416, i.e. both pond and meadow soil cores) matrix. Coordinates of the 416 soil cores on the first four axes of the correspondence analysis were saved. This step serves to reduce the dimensionality of the data set from 77 (species) to four (number of ordination axes), while preserving the maximum amount of trended variation in the data structure. A mean ordination score (for each of the four CA axes) was then calculated for the pond and meadow seed banks to produce two four-variable vectors. These two vectors were compared statistically using the multivariate T^2 test (Morrison 1990, p. 140-144). If the meadow and pond seed banks are similar, scores for the two groups would overlap on all ordination axes and as a result the two mean vectors would not be significantly different. If however the seed banks are different, two distinct groups will be present in the ordination space and the mean vectors will therefore be significantly different. The same procedure was used to compare the seed bank of the cold and non-cold treatments of the meadow soil cores.

4.3 Results

Full Ponds

Nature of the soil seed bank

The seed banks of the full ponds were quite different from the vegetation found along the river corridor. The dominant species of the seed bank include annuals and "weedy" grass species such as *Poa palustris*, that are generally not abundant in the vegetation. The only species that was abundant in both vegetation and the seed banks was *Urtica dioica*. Figure 4.2a,b,c displays the changes in seed frequency between the ponds. The ponds are ordered by location (upstream to downstream). No consistent trends are apparent along the length of the river.

Species richness within the full ponds

The ANOVA comparing the number of species per soil sample indicates that there are significant differences between the seed bank richness depending on transect location and pond number (Table 4.2). The box plots are presented in figure 4.3. The species richness is greatest on transect 1 and lowest for transect 3 of the main meadow. Ponds 2, 4 and 7 have the fewest species, and pond 6 has the largest number of species.

Correspondence analysis results

The ordination of the seed bank frequencies per transect suggests that the seed bank of each individual pond is unique (Figure 4.4 and Table 4.3). Pond 2 separates out from all other ponds and appears to be "more" unique than the others. The dam associated with

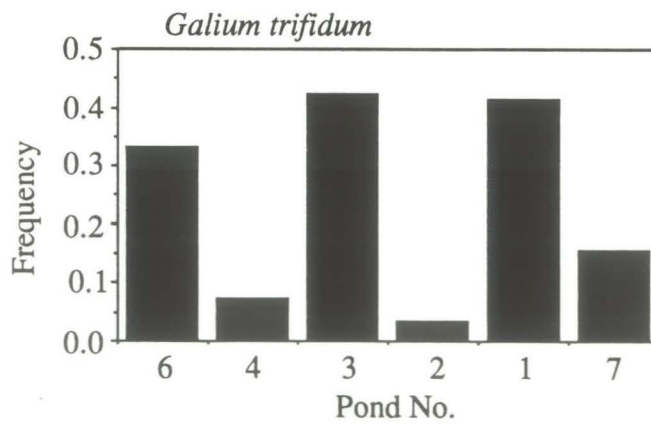
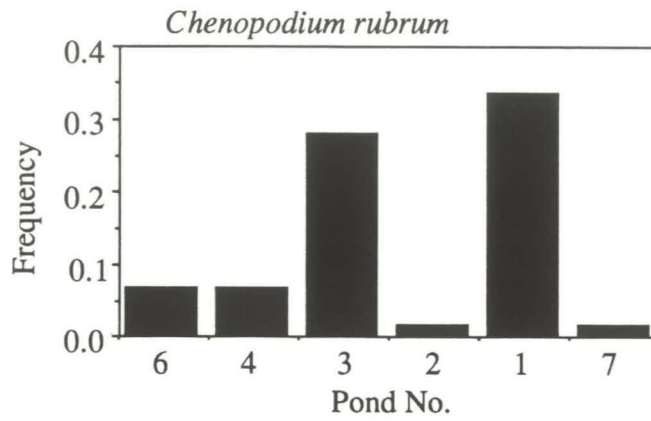
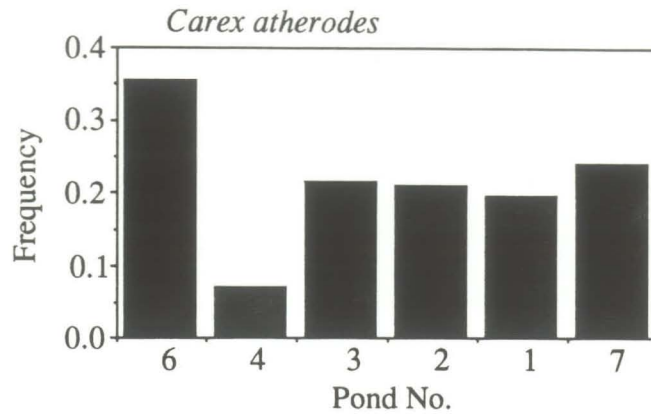


Figure 4.2a Seed frequencies by pond. Ponds are ordered from upstream to downstream.

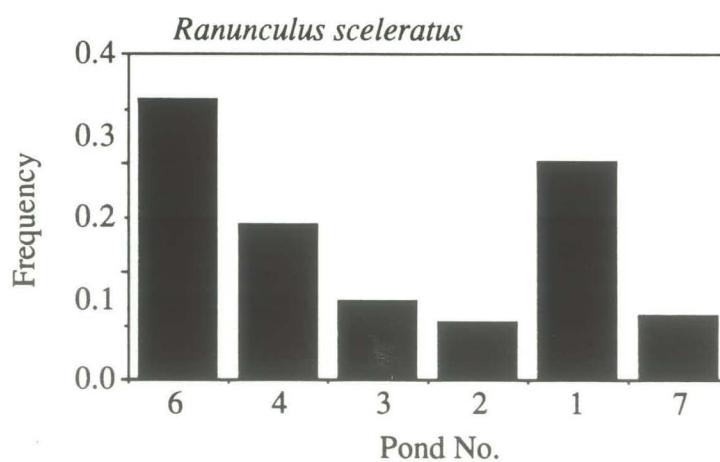
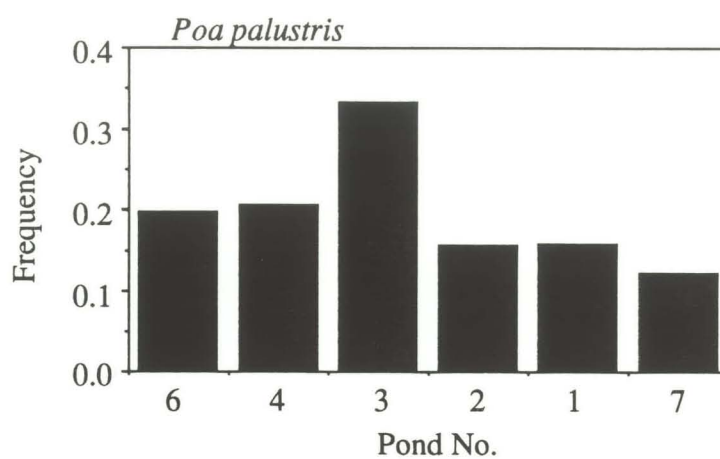
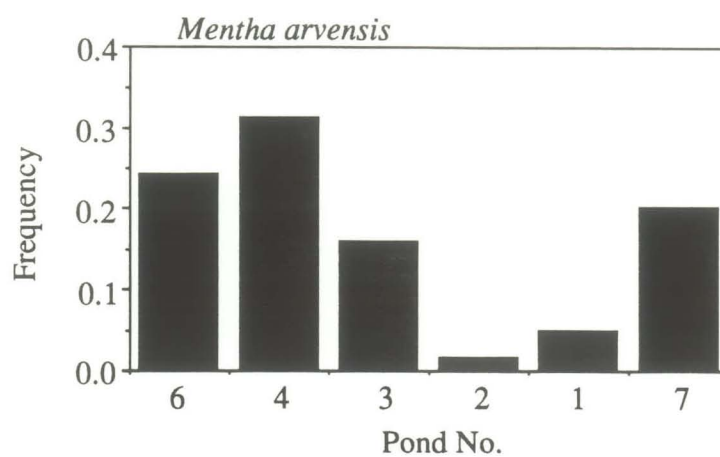


Figure 4.2b Seed frequencies by pond. Ponds are ordered from upstream to downstream.

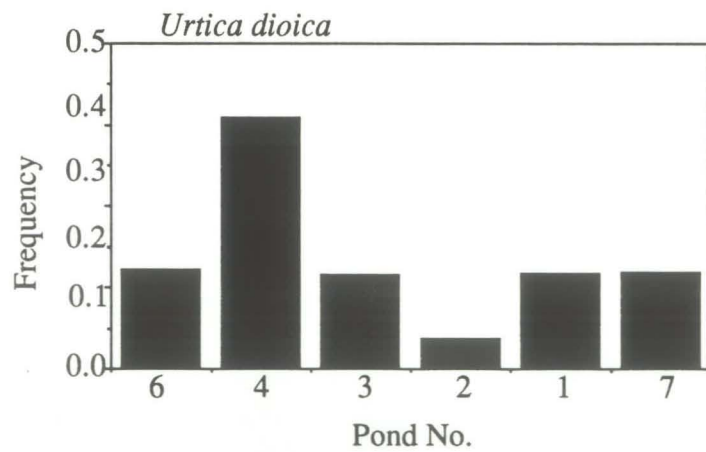
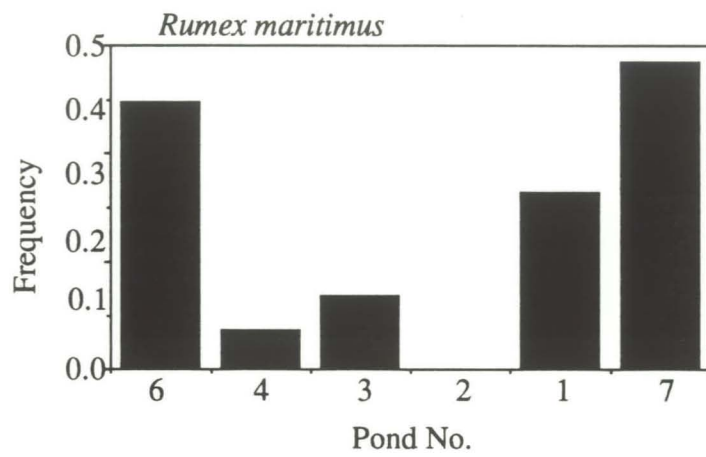
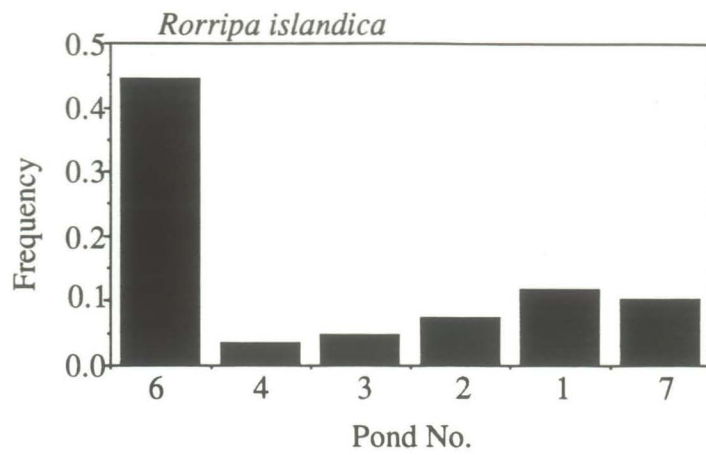


Figure 4.2c Seed frequencies by pond. Ponds are ordered from upstream to downstream.

Table 4.2 Analysis of variance for species richness per soil sample.

Analysis of variance for comparison of ponds and transects					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Pond (P)	5	145.517	29.103	9.589	0.000
Transect (T)	3	100.599	33.533	11.048	0.000
P x T	15	89.648	5.977	1.969	0.019
Error	216	655.588	3.035		
Total	239	1017.730			

Analysis of variance for comparison of meadows and transects					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Meadow (M)	10	101.500	10.150	1.946	0.047
Transect (T)	3	47.685	15.895	3.047	0.032
M x T	30	213.959	7.132	1.367	0.124
Error	109	568.650	5.217		
Total	152	932.680			

Analysis of variance for comparison of ages and transects					
Source	df	Sum of Squares	Mean Square	F-ratio	Prob
Age (A)	3	4.923	1.641	0.278	0.841
Transect (T)	3	53.525	17.842	3.022	0.032
A x T	9	57.256	6.362	1.077	0.383
Error	137	808.973	5.905		
Total	152	932.680			

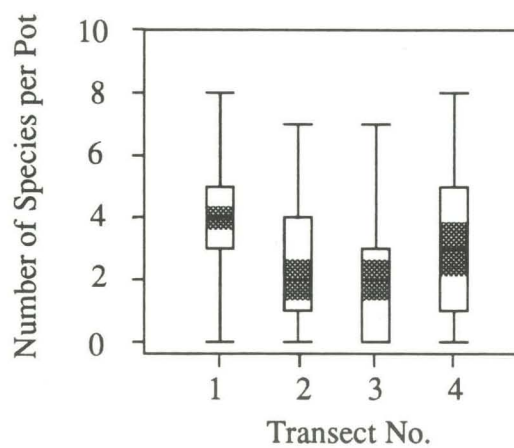
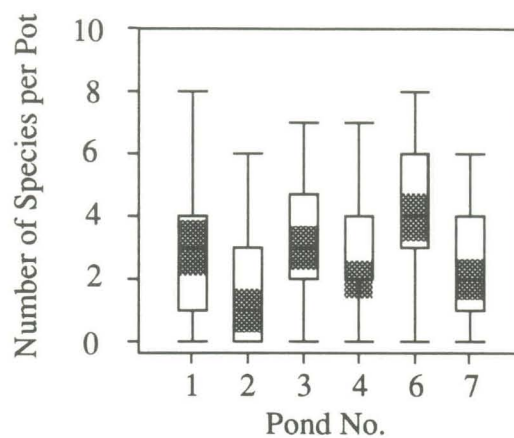


Figure 4.3 Box plots of variation in the number of species per soil sample present in the seed bank, by ponds and transect

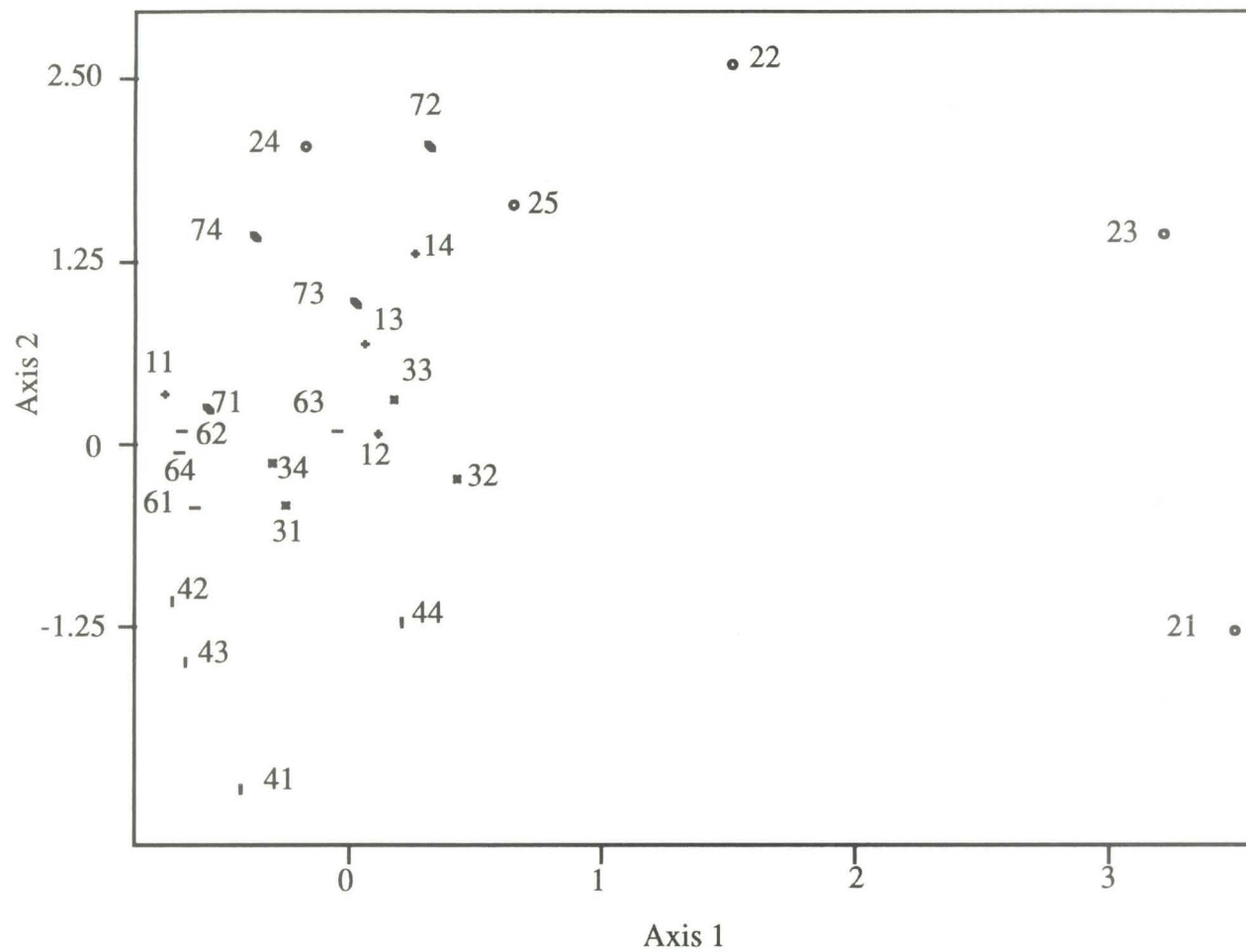


Figure 4.4 Correspondence analysis ordination of the pond seed bank transects. All ponds are included in this analysis. The first number refers to the pond and the second refers to the transect (e.g., 72 is pond 7, transect 2).

this pond is in fact a portion of a gravel road constructed by Parks Canada. Dominant seed bank species for this pond are road side weed species such as *Plantago major* which were uncommon at other sites. For this reason a second ordination was performed on the data with pond 2 removed (Figure 4.5 and Table 4.3). This ordination confirms that the seed bank of each pond is somewhat unique. The trend for transects is less clear, but it is interesting to note that, for a given pond, the first transect (i.e. dam top) always occurs as the point furthest to the right.

Table 4.3 Eigenvalues of the pond seed bank ordinations

Axes	1	2	3	4	Total inertia
Ponds including pond number 2					
Eigenvalues	.221	.190	.169	.126	1.480
Cumulative percentage variance of species data	15.0	27.8	39.2	47.7	
Ponds without pond number 2					
Eigenvalues	.262	.240	.182	.167	1.848
Cumulative percentage variance of species data	14.2	27.2	37.0	46.1	

Beaver meadows

Species richness within the meadows

As in the ponds, the number of species per soil sample is significantly different depending on both transect and meadow (Table 4.2 and Figure 4.6). However, in contrast to the ponds, transect 1, the dam top, has the lowest number of species per sample. There is a trend of gradually increasing species richness with increasing distance from the dam top. There is also a marginally significant difference between the meadows ($p=0.047$). Frequencies of common seed bank species in the meadow are presented in Figure 4.7.

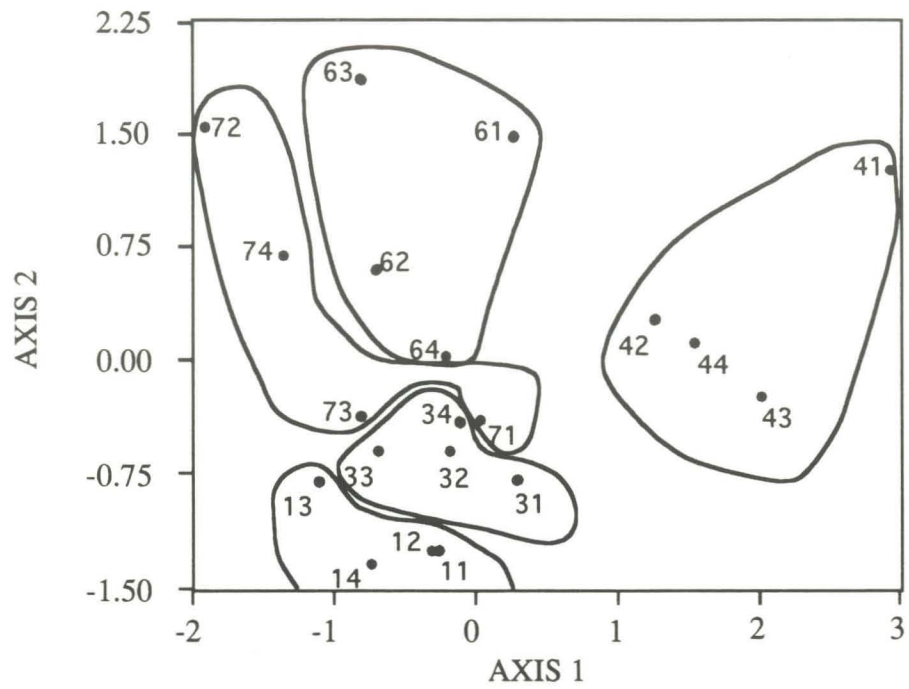


Figure 4.5: Correspondence analysis ordination of pond seed bank transects with pond number 2 excluded from the plot. The values next to the points correspond to the pond number and the transect number (e.g., 32 is pond 3, transect 2).

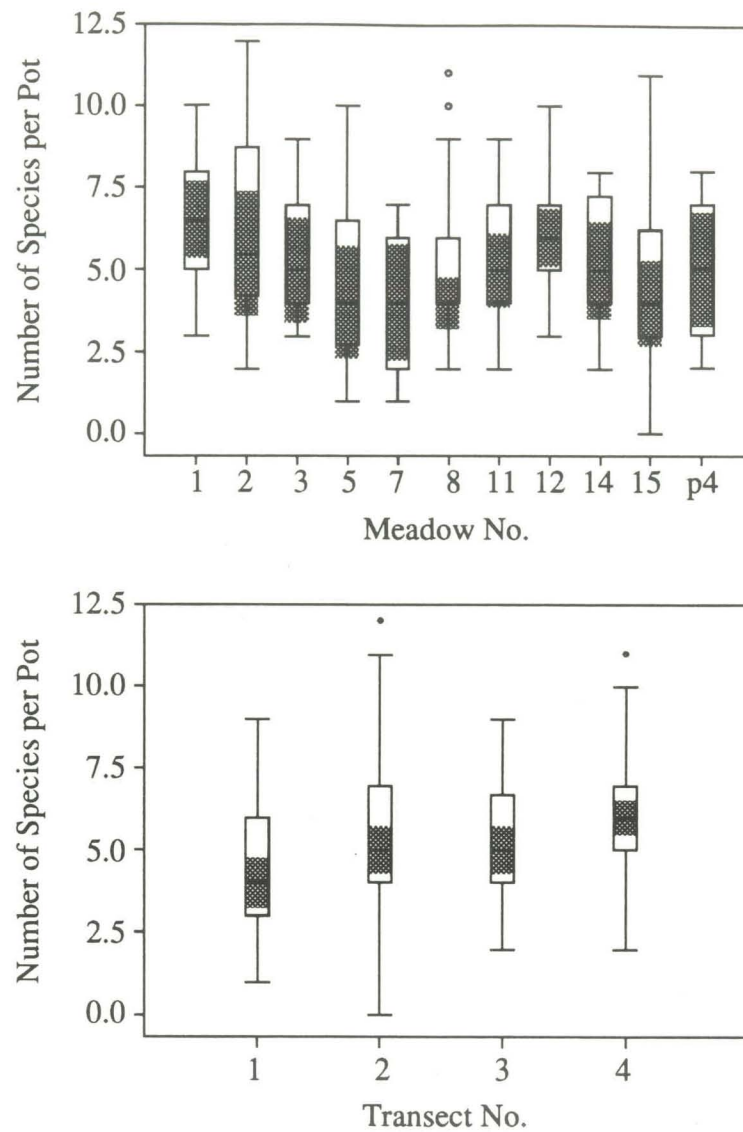


Figure 4.6 Box plots of variation in the number of species present in the seed bank of the meadows, by transect and individual meadow.

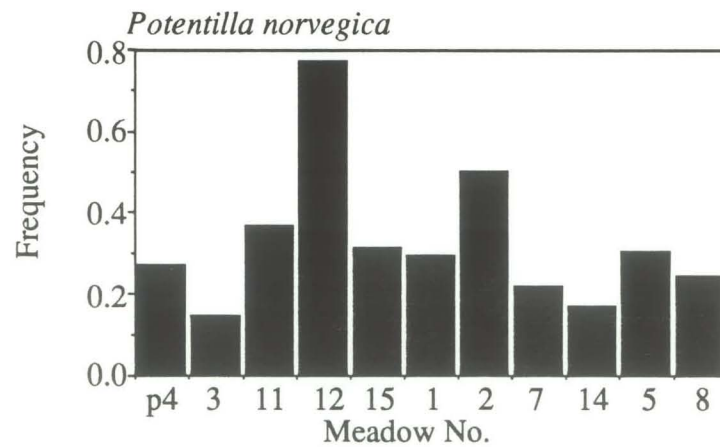
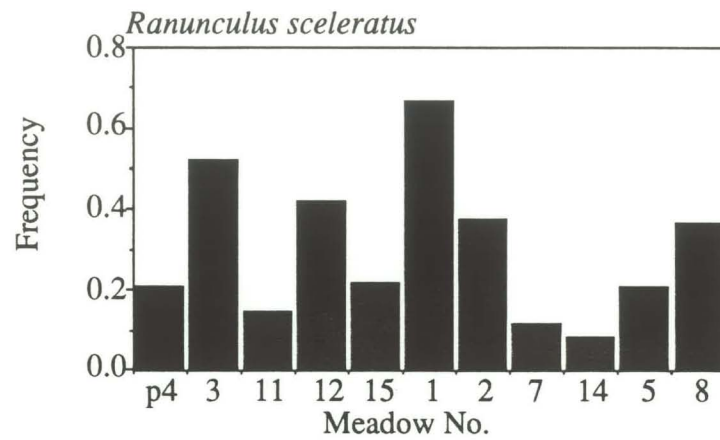
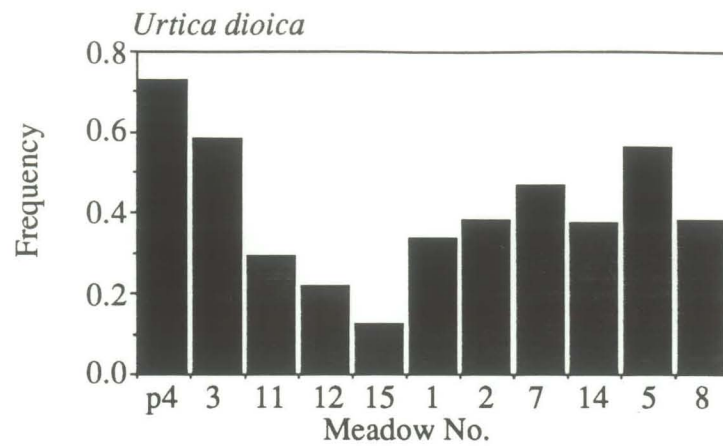


Figure 4.7a Mean frequency of species in the seed bank of individual meadows. Meadows are ordered by age.

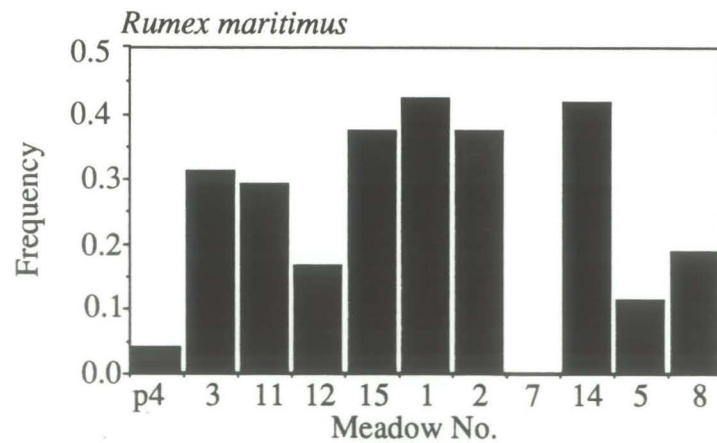
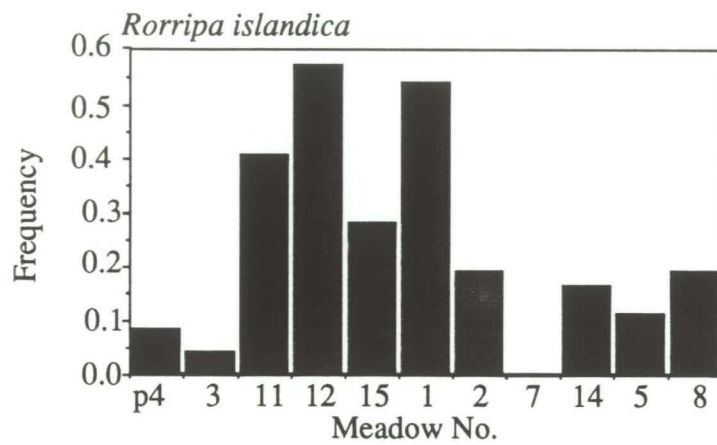
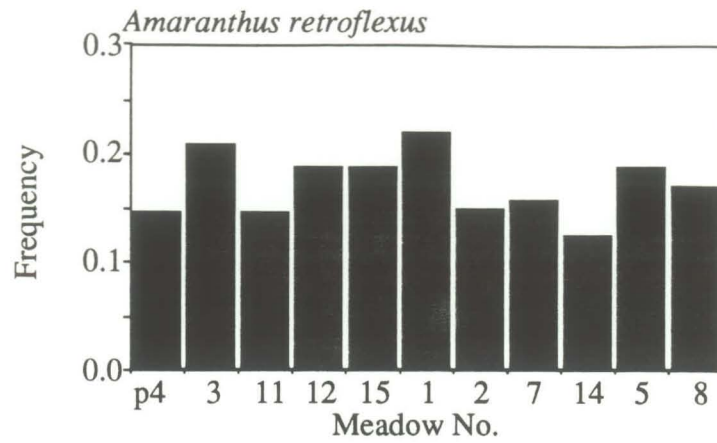


Figure 4.7b Mean frequency of species in the seed bank of individual meadows. Meadows are ordered by age.

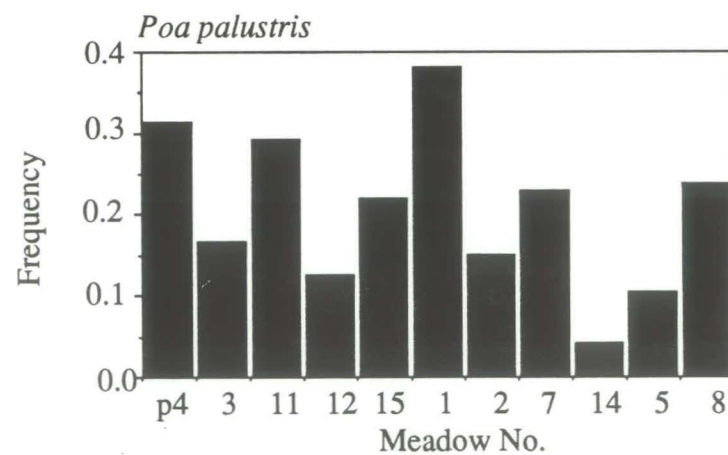
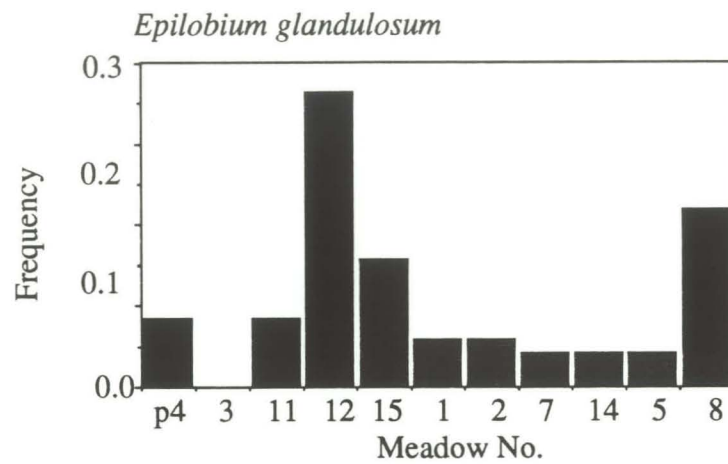
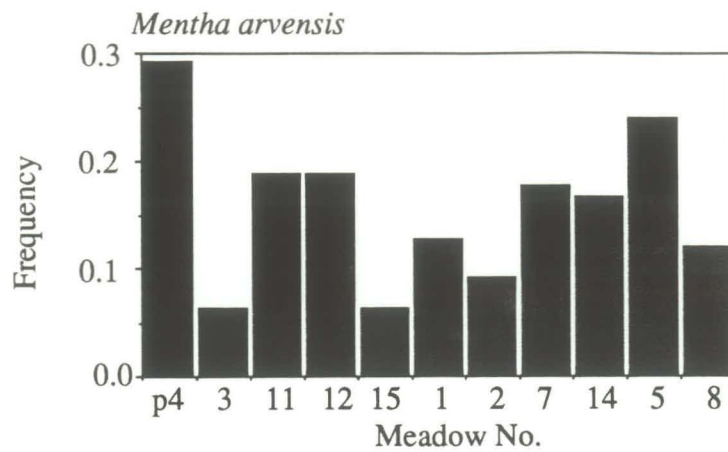


Figure 4.7c Mean frequency of species in the seed bank of individual meadows. Meadows are ordered by age.

Cold vs. non-cold treatments

The two types of meadow seed bank determination were tested for difference in results. The T^2 result indicates that there is a significant difference between them ($F = 5.9$, $p < 0.05$). A paired t-test comparing differences in frequency of all species also indicated that there was a significant difference in the species frequencies ($t = 6.226$, $p < 0.001$) (Table 4.4).

Meadow Age

The species richness of the different age classes was also examined with a two factor ANOVA (Table 4.2 and Figure 4.8). There is no significant difference between the different age categories. Frequency of common seed bank species by meadow age are presented in Figure 4.9. Some species appear to be more common in the youngest meadow (eg *Urtica dioica*, *Mentha arvensis*, *Poa palustris*), but most species showed little systematic variation with age.

Correspondence analysis results

The correspondence analysis of the eleven meadows does not appear to show any ordering by age (Figure 4.10). The ordination of the transects is not presented here as it showed no trend in age or transect location within the meadows.

Comparison of the seed banks of full ponds and meadows

The T^2 test indicated that there is a significant difference between the seed bank recorded from the full ponds and the meadows ($F = 101$, $p < 0.001$).

Table 4.4 Mean frequencies of the seeds bank in the cold and non-cold treated samples.

Species	Non Cold	Cold	Species	Non cold	Cold
<i>Agrostis scabra</i>	0.038	0.011	<i>Lycopus uniflorus</i>	0.011	0
<i>Alopecurus aequalis</i>	0	0.019	<i>Mentha arvensis</i>	0.145	0.161
<i>Amaranthus retroflexus</i>	0	0.344	<i>Plantago major</i>	0.018	0
<i>Anemone canadensis</i>	0.007	0	<i>Poa palustris</i>	0.307	0.11
<i>Aster simplex</i>	0	0.009	<i>Poa trivialis</i>	0.005	0
<i>Beckmannia syzigachne</i>	0.03	0.047	<i>Polygonum amphibium</i>	0.052	0
<i>Bidens cernua</i>	0.029	0.025	<i>Polygonum lapathifolium</i>	0	0.039
<i>Bromus inermis</i>	0	0.017	<i>Potentilla norvegica</i>	0.32	0.334
<i>Calamagrostis canadensis</i>	0.005	0	<i>Ranunculus sceleratus</i>	0.332	0.293
<i>Carex aquatilis</i>	0.023	0.073	<i>Rorippa islandica</i>	0.258	0.222
<i>Carex atherodes</i>	0.065	0.043	<i>Rumex maritimus</i>	0.298	0.205
<i>Carex sp A</i>	0	0.016	<i>Scutellaria galericulata</i>	0.007	0
<i>Carex sp B</i>	0.011	0	<i>Setaria viridis</i>	0	0.03
<i>Carex rostrata</i>	0.028	0.007	<i>Sium suave</i>	0.032	0.018
<i>Carex sp C</i>	0.041	0	<i>Solidago canadensis</i>	0.007	0.011
<i>Carex sychnocephala</i>	0.011	0.016	<i>Sonchus arvensis</i>	0.054	0.007
<i>Chenopodium rubrum</i>	0.117	0.043	<i>Sonchus asper</i>	0	0.014
<i>Chenopodium album</i>	0	0.025	<i>Spiraea sp.</i>	0	0.007
<i>Cicuta bulbifera</i>	0	0.011	<i>Stachys palustris</i>	0.007	0.019
<i>Cirsium arvense</i>	0.082	0.035	<i>Stellaria crassifolia</i>	0.018	0
<i>Crepis tectorum</i>	0	0.007	<i>Taraxacum officinale</i>	0	0.014
<i>Dracocephalum sp.</i>	0	0.04	<i>Thlaspi arvense</i>	0	0.005
<i>Eleocharis sp.</i>	0.004	0	<i>Typha latifolia</i>	0.004	0.026
<i>Epilobium glandulosum</i>	0.108	0.102	<i>Urtica dioica</i>	0.436	0.369
<i>Fragaria sp.</i>	0	0.021	<i>Vicia americana</i>	0.007	0
<i>Galeopsis tetrahit</i>	0.025	0.005	Species g	0	0.073
<i>Galium trifidum</i>	0.104	0.071	Mint x	0.005	0
<i>Geum aleppicum</i>	0	0.018	Mustard x	0	0.012
<i>Geum sp.</i>	0.02	0	Plant x	0	0.007
<i>Glyceria striata</i>	0.189	0	Grass X	0	0.007
<i>Hordeum jubatum</i>	0	0.005	Grass Y	0.012	0
<i>Juncus alpinus</i>	0.007	0.012	Species b	0	0.014
<i>Juncus dudleyi</i>	0	0.009	Species c	0	0.018
<i>Juncus filiformis</i>	0	0.007	Species e	0.007	0.005
<i>Juncus nodosus</i>	0	0.027	Species f	0.005	0
<i>Lycopus americanus</i>	0	0.01	Species q	0.007	0

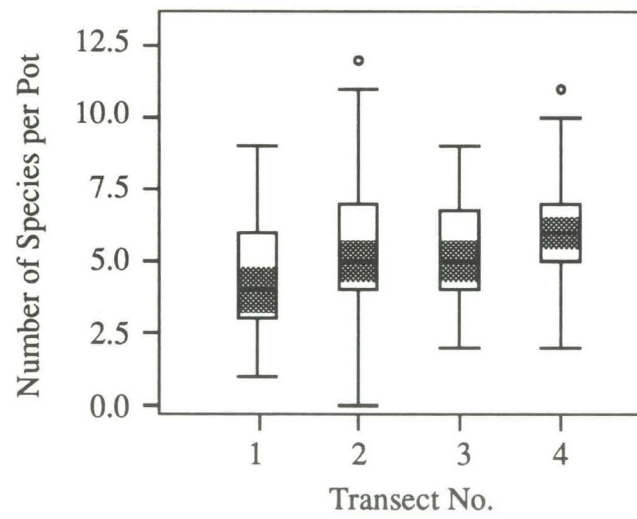
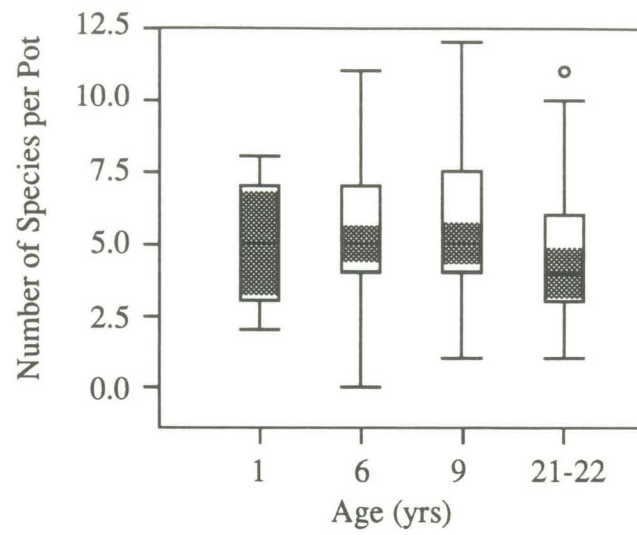


Figure 4.8 Box plots of variation in the number of species present in the seed bank per soil sample, by meadow and transect.

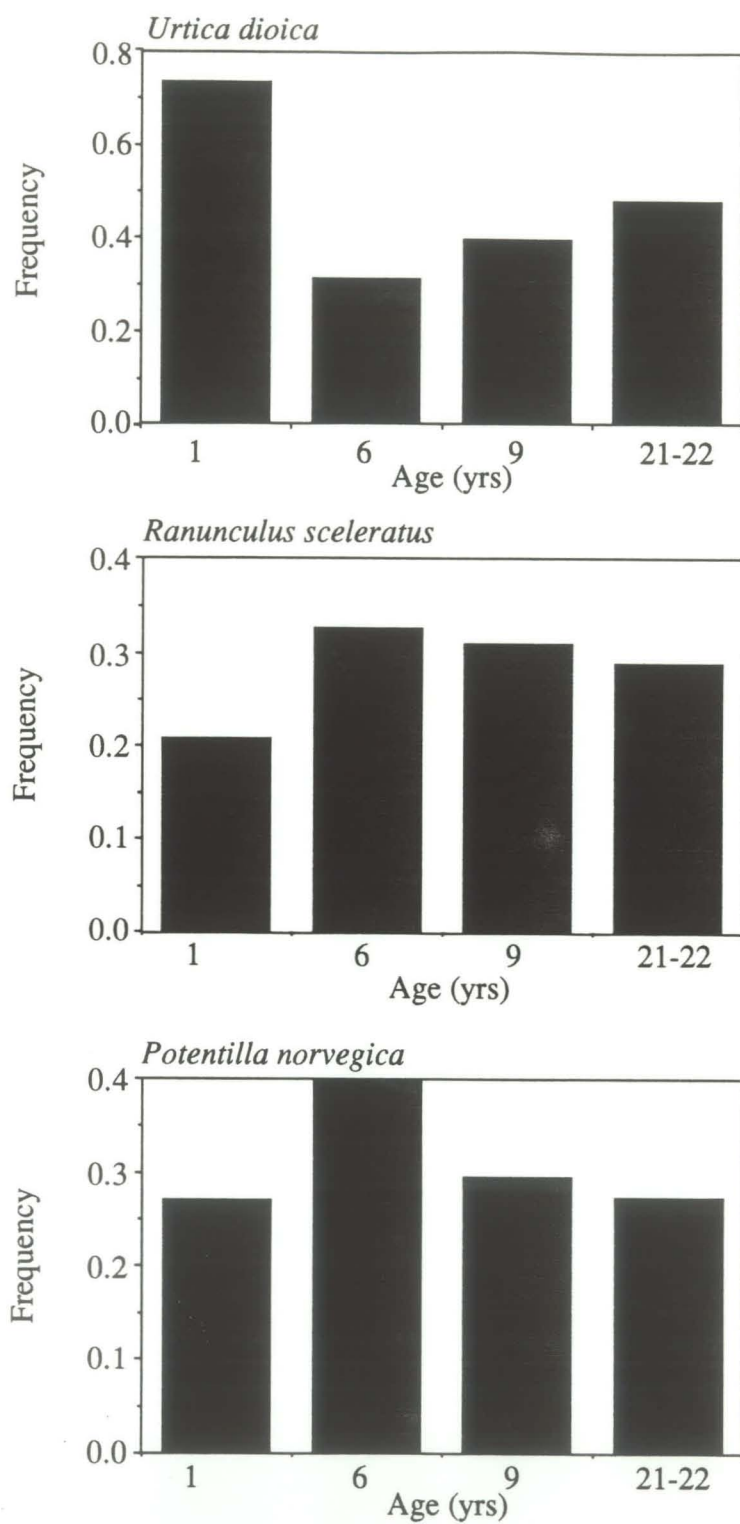


Figure 4.9a Mean frequency of species in the meadow seed banks summarized by age.

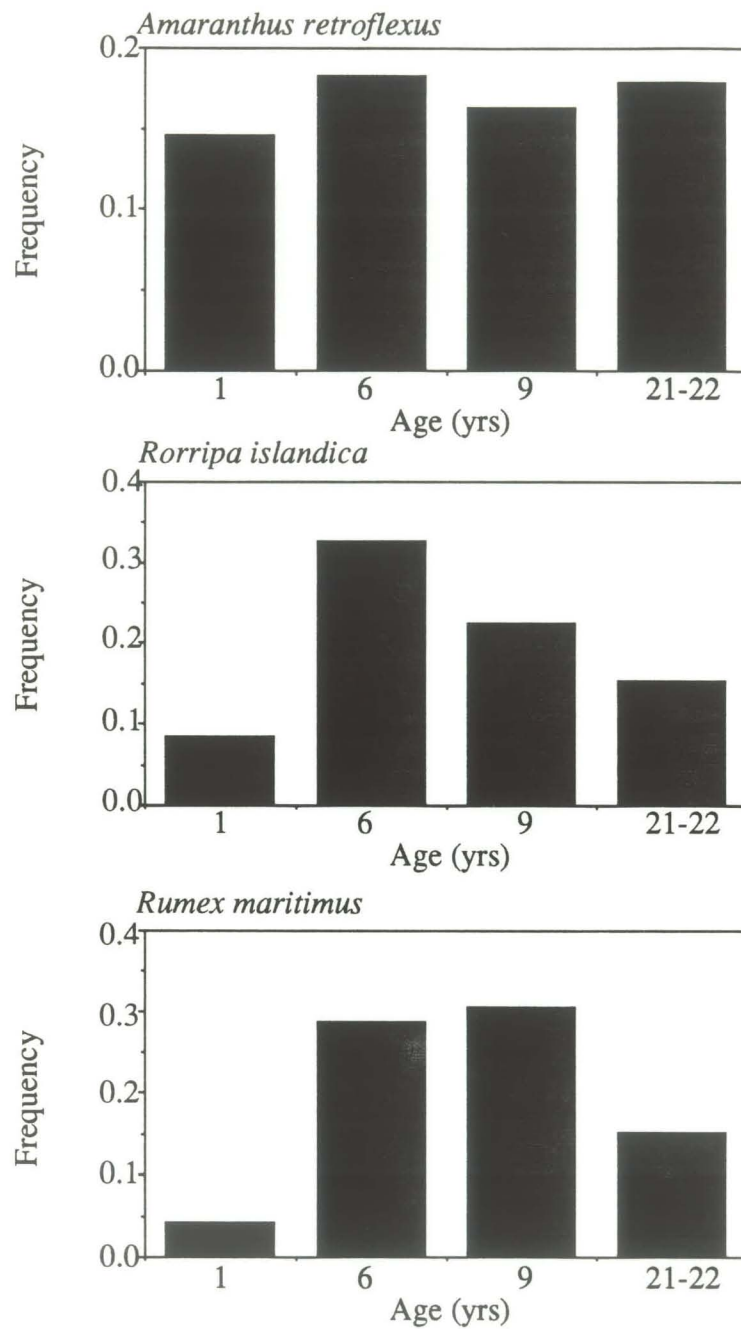


Figure 4.9b Mean frequency of species in the meadow seed banks summarized by age.

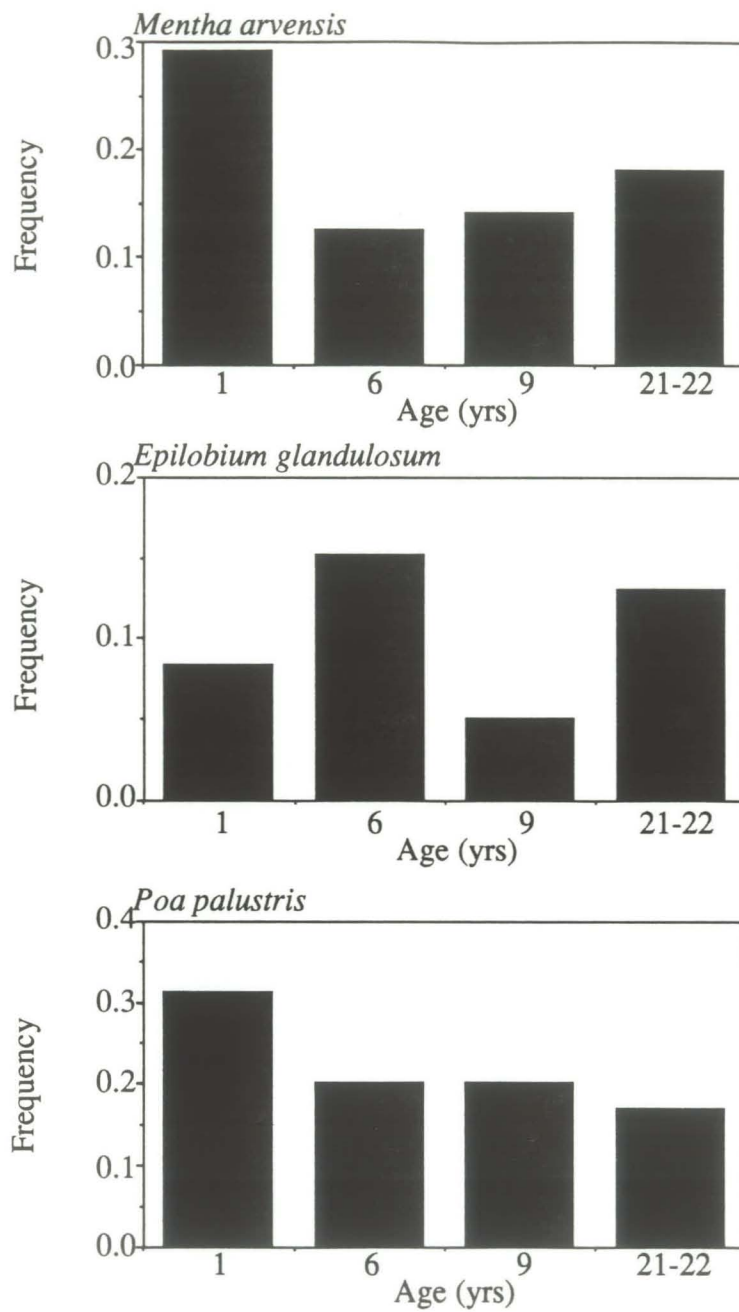


Figure 4.9c Mean frequency of species in the meadow seed banks summarized by age.

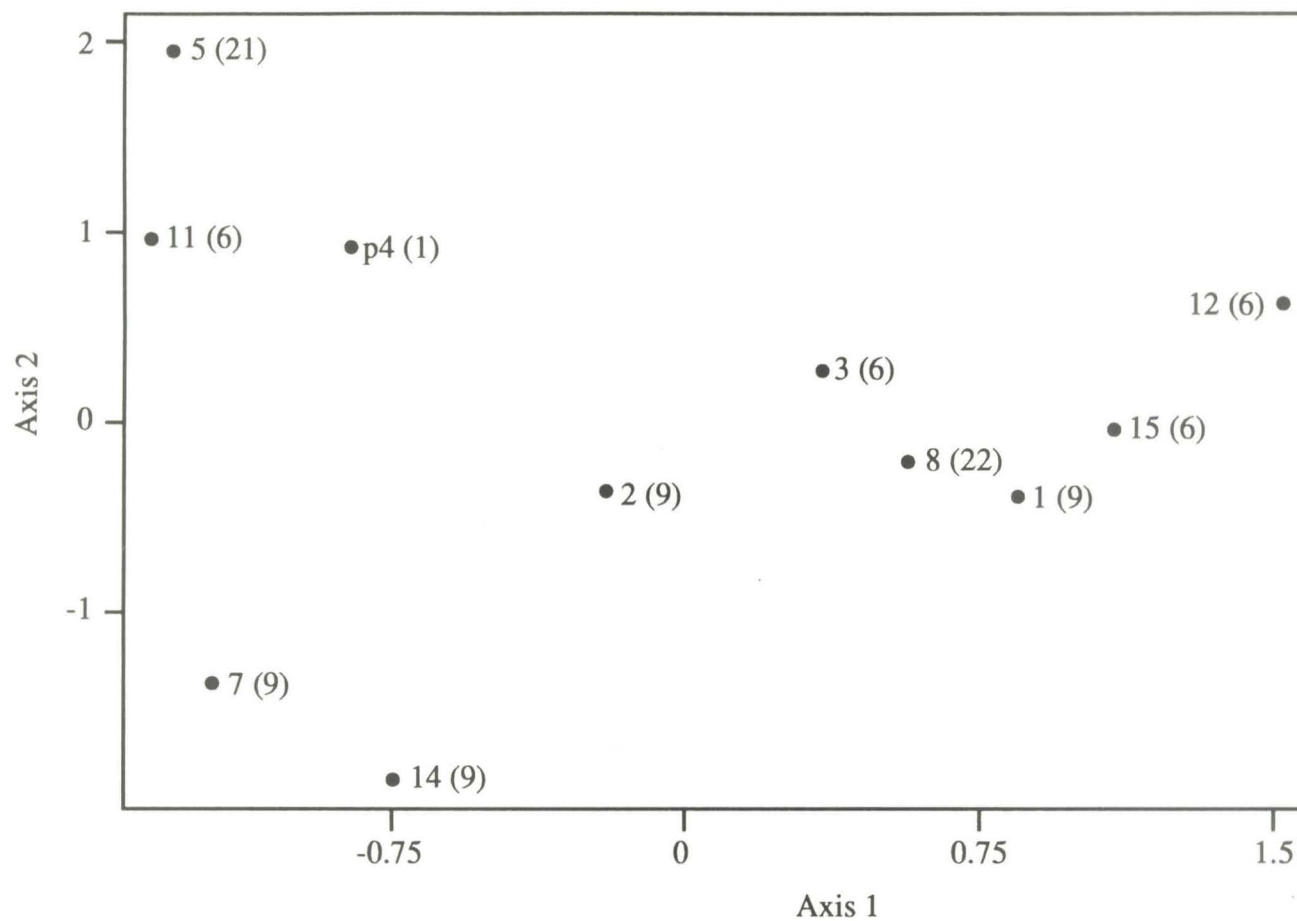


Figure 4.10 Correspondence analysis ordination of the meadow seed banks. This includes the data from the cold and non cold treated seed banks. The numbers indicate the meadow number (age).

Mean frequencies of seed bank species indicate an overall lack of correspondence between the meadow and pond seed banks (Table 4.5). A t-test performed indicated that there is a significantly larger number of species per volume soil in the meadow seed banks ($t= 5.03$, $p<0.05$).

4.4 Discussion

Full Ponds

The concept of unidirectional flow in riverine systems has led to the development of the river continuum theory (Wetzel 1983). This theory recognizes that the factors of an upstream aquatic environment will be 'passed on', to a greater or lesser extent, to downstream portions of the watercourse. Anything added to the water column (e.g., leaf litter, insect larvae, seeds and other propagules) has the potential to move considerable distances downstream (i.e. unidirectionally). When beaver dams and ponds occur along first to fifth order streams, water flow is blocked and downstream movement of materials is stopped. It has been reported (Smith et al. 1991, Naiman & Melillo 1984) that beaver ponds lead to dramatic increases in the amount of particulate matter falling out of the water column. It seems likely that seeds moving downstream would also fall out of the water column, leading to the accumulation of a soil seed bank in beaver ponds. This continual input of seed into the pond sediment ensures a 'healthy' and highly diverse seed bank, which will quickly colonize exposed mudflats following the breaching of a beaver dam. One might also expect that the seed banks of adjacent ponds might be more similar to one another than ponds that are farther apart along the watercourse. There is some evidence for this for the ponds sampled in this study. Specifically, the ordering of ponds along the first axis of the

Table 4.5 The mean frequency of all species found in the seed bank of the meadows and the ponds.

Species	Meadow	Pond	Species	Meadow	Pond
<i>Agrostis scabra</i>	0.024	0	<i>Mimulus ringens</i>	0	0.064
<i>Alopecurus aequalis</i>	0.01	0	<i>Picae glauca</i>	0	0.004
<i>Amaranthus retroflexus</i>	0.172	0	<i>Plantago major</i>	0.009	0.018
<i>Alnus incana</i>	0	0.029	<i>Poa palustris</i>	0.208	0.387
<i>Anemone canadensis</i>	0.004	0.008	<i>Poa trivialis</i>	0.003	0
<i>Aster justiformis</i>	0	0.045	<i>Polygonum amphibium</i>	0.026	0
<i>Aster simplex</i>	0.004	0	<i>Polygonum lapathifolium</i>	0.019	0.02
<i>Beckmannia syzigachne</i>	0.038	0.015	<i>Potentilla norvegica</i>	0.327	0.028
<i>Bidens cernua</i>	0.027	0.064	<i>Ranunculus aquatilis</i>	0	0.004
<i>Bromus inermis</i>	0.008	0	<i>Ranunculus sceleratus</i>	0.313	0.128
<i>Calamagrostis canadensis</i>	0.003	0.017	<i>Rorripa islandica</i>	0.24	0.134
<i>Carex aquatilis</i>	0.048	0.215	<i>Rubus strigosus</i>	0	0.004
<i>Carex atherodes</i>	0.054	0.117	<i>Rumex maritimus</i>	0.251	0.128
<i>Carex sp A</i>	0.008	0	<i>Rumex occidentalis</i>	0	0.007
<i>Carex sp B</i>	0.005	0	<i>Sagittaria cuneata</i>	0	0.016
<i>Carex rostrata</i>	0.018	0.045	<i>Salix gracilis</i>	0	0.004
<i>Carex sp C</i>	0.021	0.017	<i>Scutellaria galericulata</i>	0.004	0
<i>Carex sychnocephala</i>	0.013	0	<i>Setaria viridis</i>	0.015	0
<i>Chenopodium rubrum</i>	0.08	0.126	<i>Sium suave</i>	0.025	0.039
<i>Chenopodium album</i>	0.012	0	<i>Solidago canadensis</i>	0.009	0.013
<i>Cicuta bulbifera</i>	0.005	0	<i>Sonchus arvensis</i>	0.031	0.044
<i>Cirsium arvense</i>	0.058	0.032	<i>Sonchus asper</i>	0.007	0
<i>Crepis tectorum</i>	0.004	0	<i>Spiraea sp.</i>	0.004	0
<i>Dracocephalum sp</i>	0.02	0	<i>Stachys palustris</i>	0.013	0.027
<i>Eleocharis sp</i>	0.002	0	<i>Stellaria crassifolia</i>	0.009	0
<i>Epilobium glandulosum</i>	0.105	0.023	<i>Taraxacum officinale</i>	0.007	0.009
<i>Fragaria sp</i>	0.011	0.173	<i>Thlaspi arvense</i>	0.003	0.003
<i>Galeopsis tetrahit</i>	0.015	0.018	<i>Typha latifolia</i>	0.015	0.007
<i>Galium trifidum</i>	0.087	0.23	<i>Urtica dioica</i>	0.403	0.264
<i>Geum aleppicum</i>	0.009	0.004	<i>Vicia americana</i>	0.004	0.004
<i>Geum sp</i>	0.01	0	Species b	0.007	0
<i>Glyceria striata</i>	0.094	0	Species c	0.009	0
<i>Hoedium jubatum</i>	0.003	0	Species e	0.006	0
<i>Juncus alpinus</i>	0.01	0	Species f	0.003	0
<i>Juncus dudleyi</i>	0.004	0	Species q	0.004	0
<i>Juncus filiformis</i>	0.004	0	Species g	0.036	0
<i>Juncus nodosus</i>	0.013	0	Grass x	0.004	0
<i>Lycopus americanus</i>	0.005	0	Grass y	0.006	0
<i>Lycopus uniflorus</i>	0.005	0.021	Mustard x	0.006	0
<i>Medicago lupulina</i>	0	0.01	Mint x	0.003	0
<i>Mentha arvensis</i>	0.153	0.158			

ordination (Fig. 4.5) corresponds quite well to the location of the ponds along the river corridor. Ponds 6, 4 and 3 are the most upstream, while ponds 1 and 7 are the furthest downstream. The ordination results indicate that the seed bank of each pond is somewhat unique, and that location along the river has some effect on seed bank composition. Such results are consistent with the river continuum theory, and indicates that river flow plays an important role in seed dispersal in these systems.

Some tentative conclusions can be reached regarding the manner by which the seed bank of a beaver pond develops and is perpetuated. The local seed rain in the immediate pond area is likely a primary contributor to the seed bank, and would result in each pond having a somewhat unique species composition. Seed may also enter the pond sediments via the river 'corridor' that transports seed from upstream areas. This would result in seed banks of adjacent ponds being more similar to one another than those of ponds that are more spatially separated.

Beaver Meadows

Whereas beaver ponds must ultimately receive seed from the water column, the seed bank of beaver ponds has a number of inputs (e.g., seed rain, water column during periodic flooding, animal-transported seed). Seed arriving in pond vs. meadow locations might be expected to differ in their survivability due to differences in prevailing environmental conditions. Specifically, the sediment of full ponds is generally anaerobic (Naiman & Melillo 1984), whereas that of meadows is quite moist but rarely anaerobic. This could result in differences in seed viability and longevity between ponds and meadows. The broader range of input sources, and improved environmental conditions for seed survival, might be expected to result in a more diverse seed bank population in meadow systems as was found in this study.

My results indicate that there were few if any differences in seed banks between the meadows, regardless of age (Fig. 4.3). This suggests that the soil seed bank environment of the meadows remains similar over time, and that the distribution of seed rain throughout the meadow complex is remarkably uniform. This uniformity of seed bank composition in beaver meadows may be largely attributable to spring flooding that occur throughout the river valley. Flooding occurs over a wide portion of the valley floor, including the meadows examined in this study. The greatest abundance of viable seeds are contained within the top few cm of soil (Baskin & Baskin 1989), and periodic flooding is expected to cover the substrate with seed-containing sediment. Over time, this would tend to 'homogenize' seed bank composition along the entire river corridor.

4.5 Summary

- (1) The seed banks of both the beaver ponds and meadows are dominated by annuals and short-lived, non-clonal perennials.
- (2) The seed bank of each pond is somewhat unique, and there is some evidence to suggest that nearby ponds have more similar seed banks than ponds that are more spatially separated. The dam top has the highest species richness.
- (3) The seed bank of each beaver meadow site is similar, and there is no evidence of a change in the seed bank composition with increasing meadow age. In contrast to the pond sites, species richness is lowest on the dam top.
- (4) The seed bank of the ponds has significantly lower species richness than that of beaver meadows.

- (5) The seed bank composition of cold and non-cold treated soil samples from the meadow sites were significantly different in their species composition.

Chapter 5 Spatio-Temporal Vegetation Dynamics of Beaver Meadows

5.1 Introduction

Although a number of investigations have examined changes in vegetation composition and community structure resulting from beaver activity (e.g., Neff 1957; Naiman et al. 1986; Naiman 1988; Naiman et al. 1988; Barnes & Dribble 1988), the majority have focussed on the exploitation of forest trees (mainly trembling aspen) or more generally on forest vegetation dynamics. Few investigators have examined the vegetation dynamics of the beaver pond-meadow systems following the abandonment of a site by beaver. Indeed, the only available information is anecdotal in nature (see Neff 1957 and Naiman 1988). It is known that when a beaver colony depletes its supply of aspen, it abandons a site for another (usually upstream) with an abundant food supply (DeByle & Winokur 1985; Beier & Barrett 1987; Naiman et al. 1988). The abandoned beaver dam soon breaches (usually during the spring freshet), releasing the contained water and exposing a mudflat. Little is known of the vegetation changes that occur on these mudflats, however. In Minnesota, Naiman et al. (1988) observed a procession from an initial wet sedge meadow community to a drier one dominated by grasses. Such a development likely reflects a combination of change in hydrological conditions, site invasion by wind-borne seed and vegetative propagules, and interspecific competition. Shrub and tree invasion may also occur, depending on grazing frequency (both by beaver and other mammals) and soil factors (Graham 1963).

Naiman et al. (1988) proposed that beaver activity results in multi-successional pathways that may alter riverine landscapes for centuries. They recognize that the beaver-meadow complex is dynamic, with a given site moving from a pond to a meadow following site abandonment, and reverting again to a pond when the site is recolonized by beaver. This

site reversion is largely dependent on activities of the beaver population, but usually occurs within a time frame of <100 years. This cyclical change is somewhat analogous to the dynamics model for prairie marshes proposed by van der Valk & Davis (1978), but with the cycle dependent on beaver activity rather than climate (i.e. 'drawdown' cycles). Studies are required to determine the changes in vegetation composition and structure that occur following meadow site abandonment by beaver.

The objectives of this study are:

- (1) to quantify the changes in vegetation composition that occur over time in beaver meadow communities, over the entire meadows and within specific areas of the meadow (e.g., dam top, dam face, meadow proper).
- (2) to define and describe plant species ecological groups for the meadow vegetation.
- (3) to compare the composition of the soil seed bank and the extant vegetation of the beaver meadows.

5.2 Materials and Methods

Site Selection and Meadow Age Determination

Aerial photographs of Riding Mountain National Park for the period 1931-1986 were used to determine meadow ages (Table 5.1). For each beaver pond within the study area, a series of photographs over time were examined to determine the date at which the pond was last full. This was used as an 'index' of meadow age, under the assumption that the beaver pond was abandoned (and the dam breached) the following spring. Thus 'meadow age'

represents the *maximum* number of years that the site has not been underwater. As most aerial photographs are taken in July or August when small but active beaver ponds often dry out due to low streamflow, only large ponds were considered in this study. A total of eleven meadows were selected, ranging in age from 1 to 22 years. For each meadow, the photograph at which it was last filled with water was digitized using an Abaton 300/GS® scanner and processed using the image analysis programs Image Studio® 1.7 and Image® 1.41 to determine the area flooded. Table 5.2 summarizes the size and age of these eleven sites. Detailed maps of the eleven meadows are given in Appendix 2.

Vegetation Sampling

All meadows were numbered and located on 1:50,000 topographical maps. Each site was then located in the field using aerial photographs and topographical maps. Dam length was measured to aid in determining the scale of air photographs. Within each meadow a series of four or five transects was set up. The first two transects, located along the top of the abandoned dam and the bottom of the dam face respectively, are referred to as 'dam transects'. These two transects began and ended at the edges of the built-up dam portions. A third transect was located 10 m from, and perpendicular to, the dam face. One or two additional transects were located at 20 m intervals from the third transect, depending on the areal extent of the meadow. Transects 3-5, referred to as 'meadow transects', included only areas that were once flooded. Figure 5.1 illustrates the location of transects in the field.

Along each transect 50 cm x 50 cm quadrats were placed every 10 m, and the percent cover of all grasses, herbs and forbs estimated to the nearest 5%. Along the meadow transects (transects 3-5) shrub densities were also determined. At 10 m intervals along each transect, a 5m radius circle was delineated and the number and height of shrubs, by species, was determined.

Table 5.1 List of aerial photographs used in determining the age and size of the meadows.

Aerial Photo Used	Year	Month
A4341-17	31	9
A4341-18	31	9
A4341-19	31	9
A4342-3	31	9
A4342-5	31	9
A11938-338	49	6
A16845-269	59	9
A16845-271	59	9
A16845-312	59	9
A16845-313	59	9
A18631-183	64	9
A18631-185	64	9
A18631-187	64	9
A18960-138	65	7
A20507-157	69	5
A20507-159	69	5
A20587-89	69	5
A21753-19	70	7
A31175-80	78	5
A31175-83	78	5
A25982-280	82	5
A25982-44	82	5
A25983-233	82	6
A25993-211	82	6
A25993-249	82	6
A26662-74	85	5
A26963-29	86	7

Table 5.2. Area and age of the eleven meadows used in the study.

Meadow No.	Age (yrs)	Area (m ²)
p4	1	2173
3	6	5821
11	6	3867
12	6	2265
15	6	22633
1	9	7834
2	9	12909
7	9	14792
14	9	1815
5	21	6543
8	22	15636

The number of transects, and quadrats, for each of the eleven meadows is summarized in Table 5.3. A total of 358 grass-herb-forb quadrats, and 158 shrub quadrats, were enumerated.

Plant species were identified using Cody (1988) and Scoggan (1957). Nomenclature follows Scoggan (1979-80) with authorities listed in Appendix 2.7.

Data Analysis

(a) Summary Statistics

The following summary statistics were computed for the species:

- for the most abundant species, mean cover values for each of four meadow age classes (1, 6, 9, and 21-22 years since flooded).
- for the two most abundant species of the meadows (*Calamagrostis canadensis* and *Carex atherodes*), mean cover values in each of the eleven meadows.

In addition, each of the 70 non-woody species encountered in the study was assigned to one of the following growth-life form categories: (a) annuals; (b) perennials (c) grass/sedge (d) shrub Mean cover values for each of these growth-life form categories were then computed for each of the four meadow age classes.

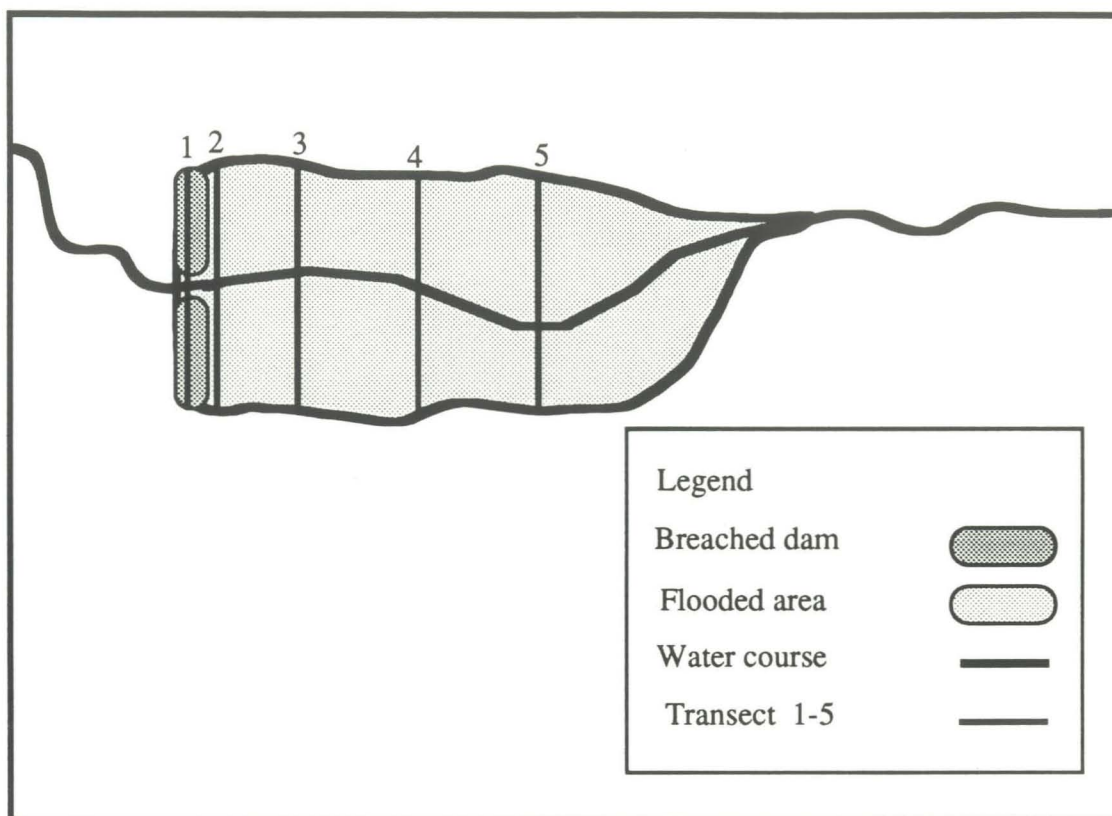


Figure 5.1: Location of transects on a drained meadow.

Table 5.3 Number of transects and samples for the vegetation portion of the study.

Meadow No.	No. Transects	No. Grass-herb-forb quadrats	No. Shrub quadrats
1	5	40	22
2	5	46	28
3	4	22	8
5	4	24	10
7	4	27	13
8	5	51	24
11	4	32	7
12	4	25	5
14	4	26	12
15	4	40	20
p4	4	25	9
Meadow total	47	358	158

(b) Canonical correspondence analysis (CCA)

This ordination method examines the relationship between two sets (thus 'canonical') of information collected on the same individuals. The method is a variant of correspondence analysis (CA, Benzecri 1990), which was described in Chapter 4. It differs in that the ordination results are 'constrained' (i.e. dependent on) a second variable set (in ecological applications, the second variable set generally consists of environmental measures). The ordination diagram produced displays the positions of the variables and individuals, as well as vectors indicating the direction and 'strength' of the environmental correlates. In the present study the individuals are the 11 meadows, and there are two variable sets: the 70 species, and 6 environmental factors. Thus the canonical model uses (a) the mean vegetation cover values (11 x 70), and (b) mean values for six 'environmental' variables (11 x 6). These six variables include five soil factors (soil moisture content, bulk density, organic content, pH and conductivity), while the sixth is meadow age. Three separate ordinations were undertaken, using the following data sets:

- mean percent cover values of species using all transects/quadrats (not including trees and shrubs).
- mean percent cover values of species using from transects 1 and 2 only ('dam transects').
- mean percent cover values of species using transects 3-5 only ('meadow transects').

All ordinations were undertaken using the program CANOCO® version 3.10 (ter Braak 1987). In all cases correspondence analysis (CA) ordinations (i.e. using only the species information, without the 'environmental' variables) were also performed. The results of CA and CCA were similar in all three cases. Given this fact, and because CCA provides additional information regarding environmental variation between meadows, only the results of CCA are presented here.

(c) Relationship between seed bank and extant vegetation

The correspondence between the seed bank and the vegetation present in each meadow was examined. The percent difference (PD) coefficient (Orlóci 1978) was computed between the seed bank (s) and the extant vegetation (v) for each meadow as:

$$PD_{sv} = \frac{\sum |X_{is} - X_{iv}|}{\sum (X_{is} + X_{iv})} \quad i = 1, p$$

where X_{is} is the frequency (range 0-1) of species i in the seed bank, and X_{iv} is the mean proportional cover (range 0-1) of the same species in the extant vegetation. The summation is over the p species found in the meadow. The one-complement of this coefficient, which is known the percent similarity coefficient (Bray & Curtis 1957; Krebs 1989, p. 304), was then computed. It ranges between zero (nothing in common) and one (identical).

5.3 Results

Meadow Age Structure

Aerial photographs taken between 1931 and 1948 revealed no beaver ponds along the Little Saskatchewan River between Whitewater Lake and Lake Audy; 1948 was the year that Parks Canada reintroduced beaver into Lake Audy (RMNP 1979). More than 30 pond sites were noted along the waterway between 1948 and 1988. It was noted that beaver ponds appear and disappear along the watercourse through time (Figure 5.2).

Vegetation Composition

A total of 81 vascular plant species were encountered in the study, including eight shrub and three tree species (Table 5.4). The highest number of species found within any single meadow was 31 in meadow eleven, while the lowest was 19 in meadow five. There is no trend in species richness with meadow age (Table 5.5).

Variations in the mean percent cover values of various life/growth form classes are presented in Figure 5.3. Annual species are abundant in the year old meadow but are relatively unimportant in the older meadows. Grass and sedge increases from 40% in the youngest meadow to 60% in the older meadows. Shrub density increases with age. A small decrease in cover of perennials (excluding grasses/sedges and shrubs) occurs with increasing age.

Changes in abundance for representative species are shown in Figure 5.4. Species that are most abundant in youngest meadows include *Galeopsis tetrahit*, *Fragaria sp*, *Sium*

suave, *Epilobium glandulosum*, *Mentha arvensis*, *Bidens cernua*, and *Galium trifidum*. These species are typically found growing most abundantly on exposed mudflats and other disturbed areas, though they persist at low abundance even in the oldest meadows. A complete list of species found on newly exposed mudflats is given in Table 5.6. Note that these are mostly annuals and short-lived, non-clonal perennials. Only a few species show increased abundance with meadow age. These include *Polygonum amphibium*, *Anemone canadensis*, *Carex rostrata*, and *Rubus strigosus*. The first two species are indicative of moist but not wet conditions, suggesting that the oldest meadow sites may be somewhat drier than younger meadows. This might be expected as organic matter accumulates over time, and as the abandoned beaver dam (which continues to hold back some water during the spring freshet) is further eroded.

A number of species showed week variation in abundance with meadow age, including the two meadow community dominants *Calamagrostis canadensis* and *Carex atherodes*, and three of the community subdominants (*Cirsium arvense*, *Urtica dioica* and *Sonchus arvensis*). All of these species do show some trends with age but not as strongly as the others mentioned. This result suggests that the dominant species in the meadow communities are either able to persist in sites that are flooded by beaver dams, or are able to very quickly invade newly drained meadows. This is discussed in more detail below, with specific reference to the two community co-dominants.

Meadow Community Dominants

In all the meadows, regardless of age, the two meadow community dominants were the grass *Calamagrostis canadensis* and the sedge *Carex atherodes*. Both species are clonal and typically form dense, monodominant stands. *C. atherodes* is characteristic of wetlands which normally dry up during the summer (MacKinnon et al. 1992), while *C. canadensis*

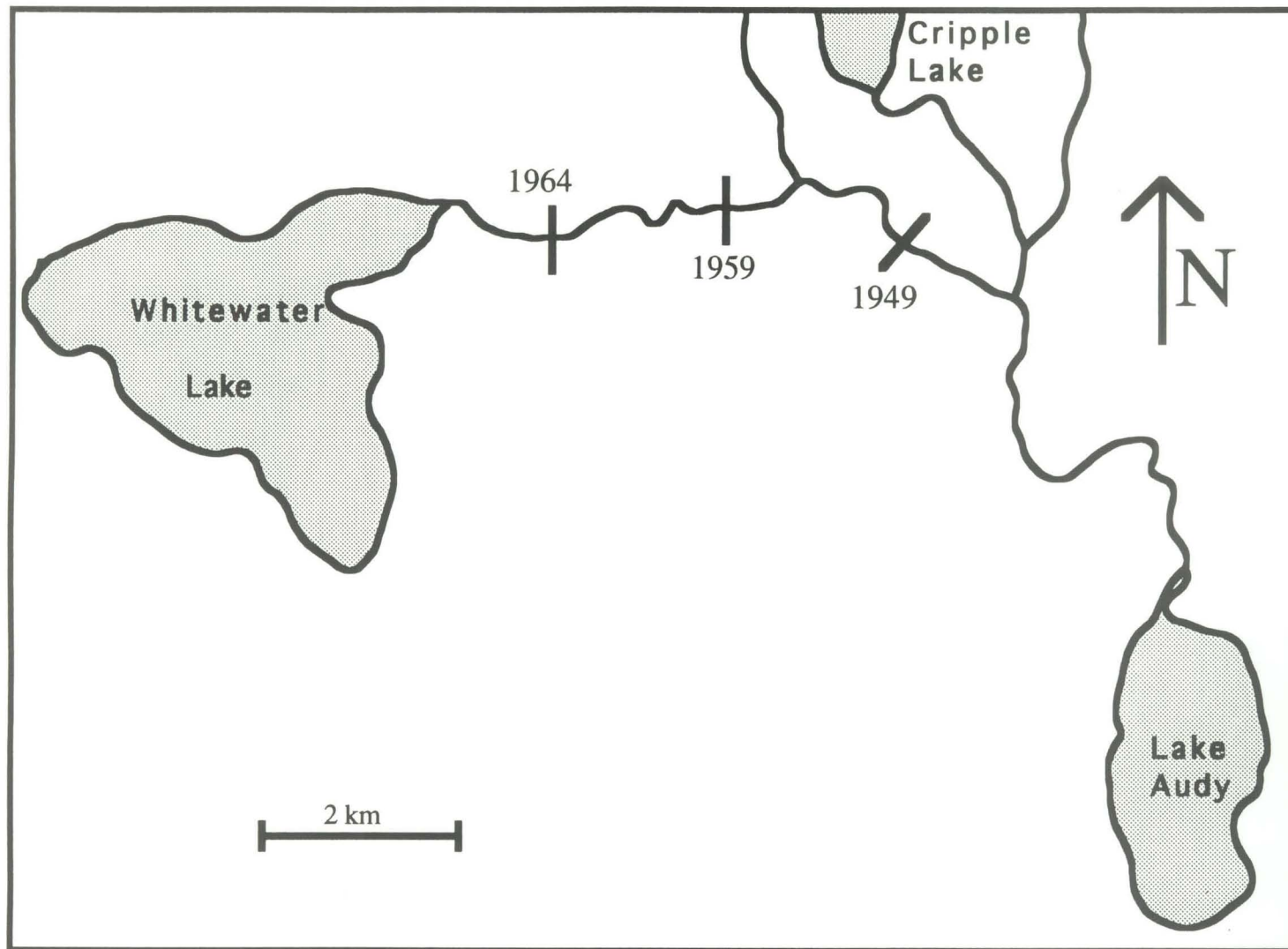


Figure 5.2. Little Saskatchewan River from Lake Audy to Whitewater Lake. The progress of the beaver upstream is presented. Each line indicates the location of the most upstream indication of beaver (ie dams) on the aerial photographs for that year. After 1964 beaver occupied the entire river system..

Table 5.4 Vascular plants found in the vegetational survey.

Perennial herbs/forbs	Annual herbs/forbs	Grasses
<i>Achillea millefolium</i>	<i>Galiopsis tetrahit</i>	<i>Calamagrostis canadensis</i>
<i>Acorus calamus</i>	<i>Galium trifidum</i>	<i>Glyceria grandis</i>
<i>Anemone canadensis</i>	<i>Lycopus asper</i>	<i>Glyceria striata</i>
<i>Aster junciformis</i>	<i>Lycopus uniflorus</i>	<i>Beckmannia syzigachne</i>
<i>Aster laevis</i>	<i>Mentha arvensis</i>	<i>Poa palustris</i>
<i>Cicuta bulbifera</i>	<i>Bidens cernua</i>	<i>Agropyron trachycaulum</i>
<i>Cirsium arvense</i>	<i>Erysimum inconspicuum</i>	<i>Agrostis scabra</i>
<i>Epilobium glandulosum</i>	<i>Habenaria hyperborea</i>	<i>Bromus ciliatus</i>
<i>Equisetum variegatum</i>	<i>Heracleum lanatum</i>	<i>Phalaris arundinacea</i>
<i>Fragaria</i> sp.	<i>Impatiens biflora</i>	<i>Phleum pratense</i>
<i>Geum aleppicum</i>	<i>Polygonum lapathifolium</i>	<i>Typha latifolia</i>
<i>Lemna minor</i>	<i>Potentilla norvegica</i>	Total 11
<i>Parnassia palustris</i>	<i>Ranunculus sceleratus</i>	
<i>Petasites palmatus</i>	<i>Rorripa islandica</i>	Sedges
<i>Petasites sagittatus</i>	<i>Rumex maritimus</i>	<i>Carex atherodes</i>
<i>Petasites</i> sp.	<i>Sparganium eurycarpum</i>	<i>Carex aquatilis</i>
<i>Plantago major</i>	Total 16	<i>Carex caespitosus</i>
<i>Polygonum amphibium</i>		<i>Carex rostrata</i>
<i>Potentilla anserina</i>		<i>Juncus balticus</i>
<i>Rudbeckia serotina</i>		<i>Scirpus caespitosus</i>
<i>Sagittaria cuneata</i>		<i>Scirpus microcarpus</i>
<i>Scutellaria lateriflora</i>	Shrubs	<i>Scirpus validus</i>
<i>Sium suave</i>	<i>Salix gracilis</i>	Total 8
<i>Solidago canadensis</i>	<i>Salix discolor</i>	
<i>Sonchus arvensis</i>	<i>Salix pedicellaris</i>	
<i>Stachys palustris</i>	<i>Betula pumila</i>	
<i>Taraxacum officinale</i>	<i>Ribes oxycanthoides</i>	Trees
<i>Urtica dioica</i>	<i>Rosa acicularis</i>	<i>Picea glauca</i>
<i>Vicia americana</i>	<i>Rubus strigosus</i>	<i>Populus balsamifera</i>
<i>Viola</i> sp.	<i>Symphoricarpos albus</i>	<i>Populus tremuloides</i>
Total 30	Total 8	Total 3

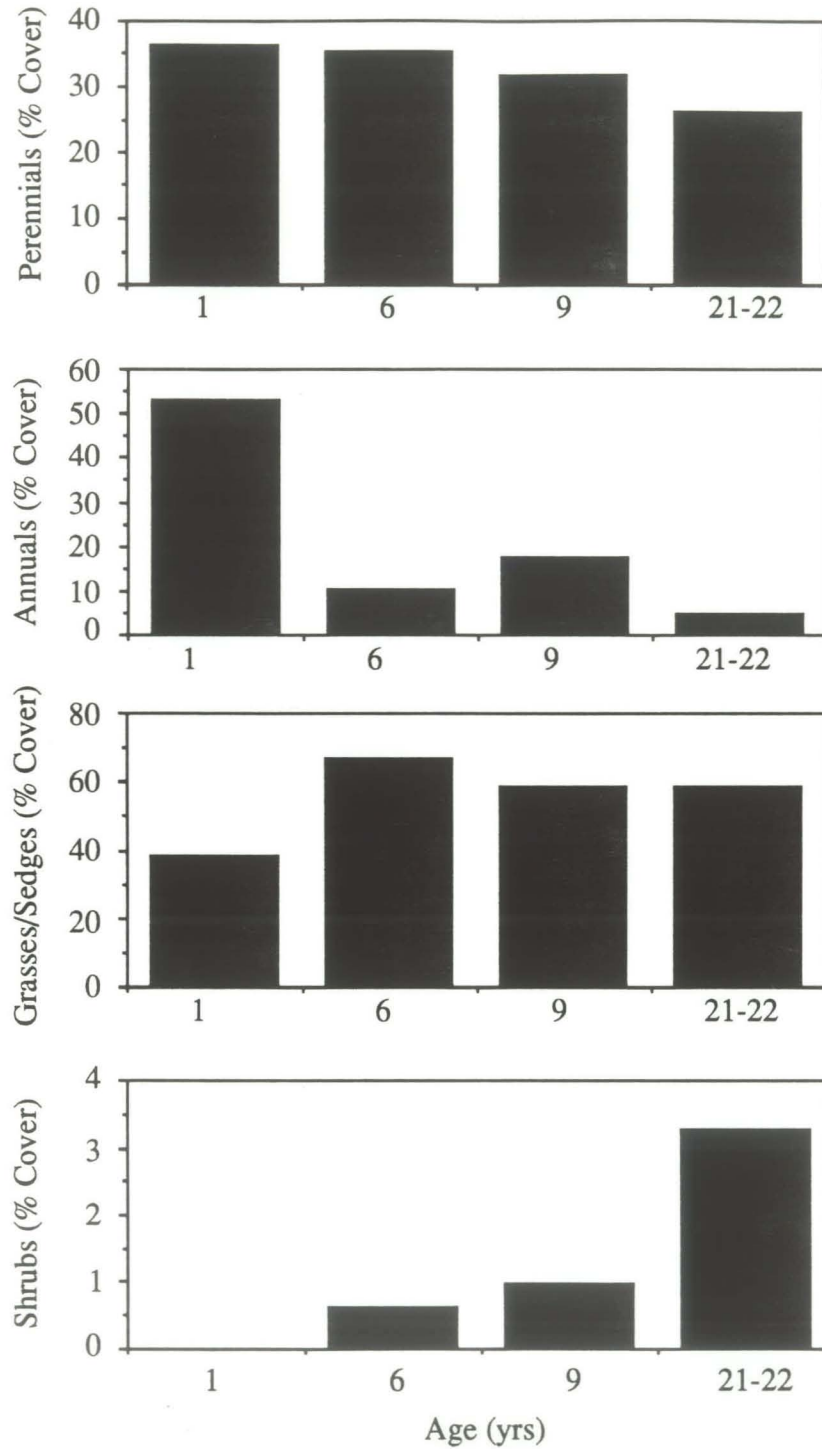


Figure 5.3 Changes in mean percent cover of four growth form - life form classes with meadow age.

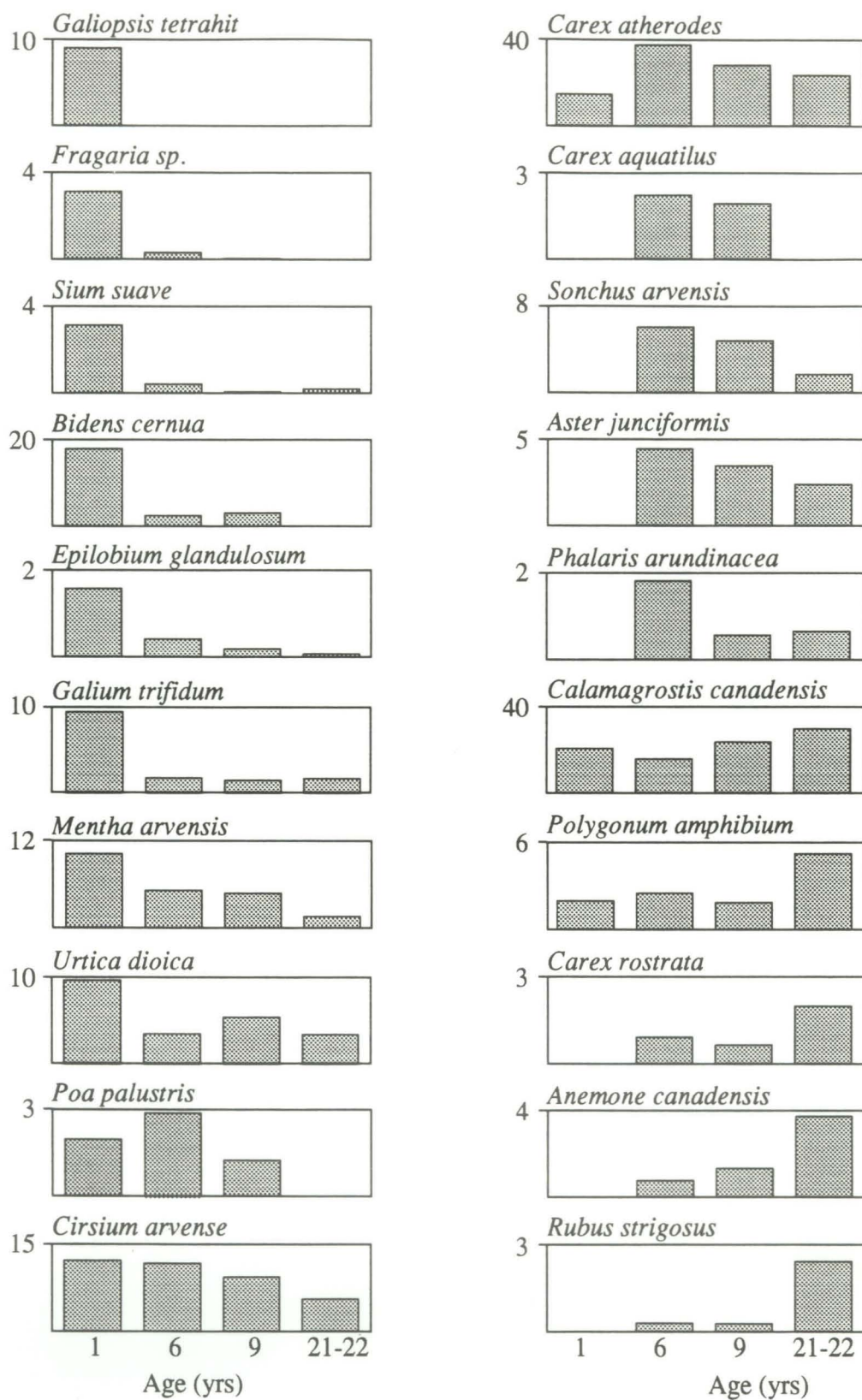


Figure 5.4 Histogram of mean percent cover by meadow age

Table 5.5 Samples taken and number of species found in the gras-herb-forb quadrates.

Meadow	Meadow Age	No. Quadrates	No. transects	No. Species
Pond 4	1	2 5	4	1 5
3	6	2 2	4	8
1 1	6	3 2	4	2 2
1 2	6	2 5	4	2 1
1 5	6	4 0	4	1 7
1	9	4 0	5	1 6
2	9	4 6	5	1 3
7	9	2 7	4	2 1
1 4	9	2 6	4	1 9
5	2 1	2 4	4	1 3
8	2 2	5 1	5	1 5
Totals		3 5 8	4 7	7 0

Table 5.6 List of species found on the mud flats and their mean cover in these location.

Species	Cover (%)
<i>Bidens cernua</i>	34.17
<i>Galium trifidum</i>	29.17
<i>Poa palustris</i>	9.17
<i>Rumex maritimus</i>	8.33
<i>Fragaria sp.</i>	7.50
<i>Galiopsis tetrahit</i>	7.50
<i>Phleum pratense</i>	6.67
<i>Rorripa islandica</i>	6.67
<i>Cirsium arvense</i>	5.83
<i>Calamagrostis canadensis</i>	5.00
<i>Epilobium glandulosum</i>	5.00
<i>Urtica dioica</i>	5.00
<i>Scirpus microcarpus</i>	4.17
<i>Ranunculus sceleratus</i>	2.50
<i>Carex aquatilis</i>	1.67
<i>Sium suave</i>	1.67
<i>Sonchus arvensis</i>	0.83

is an aggressive colonizer following disturbance (Dore & McNeill 1980). At Riding Mountain, both species were observed to produce new shoots in early May when sites are flooded (5-10 cm of standing water) and the substrate is very cold (Figure 5.5).

In most cases, a given meadow was dominated by one of *C. atherodes* and *C. canadensis* (Fig. 5.6). Differences in the community dominant were not correlated with meadow age. This again confirms previous results indicating that differences in the composition of beaver meadow vegetation shows little relation to meadow age. Another possibility is that differences in biophysical characteristics (e.g., soils, flooding regime and so forth) may determine which species dominates a given site. However, previous results have demonstrated few differences in soil conditions between the meadows, and no differences in hydrological conditions were noted (Shaw & Kenkel, pers obs.). Perhaps the community dominant (i.e. either *C. atherodes* or *C. canadensis*) is largely determined by chance. Either species, once established, will perpetuate itself at a site by strong vegetative propagation and so prevent the establishment of the other species, at least locally. However, more detailed studies may reveal microsite preferences in the two species which could better explain the dominance of one species over the other. The observation of Naiman et al. (1988) of a change from sedge-dominated to grass-dominated meadows over time (in beaver meadows in Minnesota) was not supported by this study.

Vegetation Trends with Age - Ordination Results

(a) Data from all transects

Ordination results (canonical correspondence analysis) are shown in Fig. 5.7 and Table 5.7. There is a weak age trend along the first axis, which mainly separates the one-year-old meadow from the older meadows. The one-year-old and two oldest meadows (21 and 22

Figure 5.5 a (1) *Carex atherodes* shoots emerging from the meadow substrate in early May 1991 from below about 15 cm of water. (the marks on the pole are 10 cm apart). (2) A single individual removed from the soil. (the wood is $\approx$ 20 cm wide).

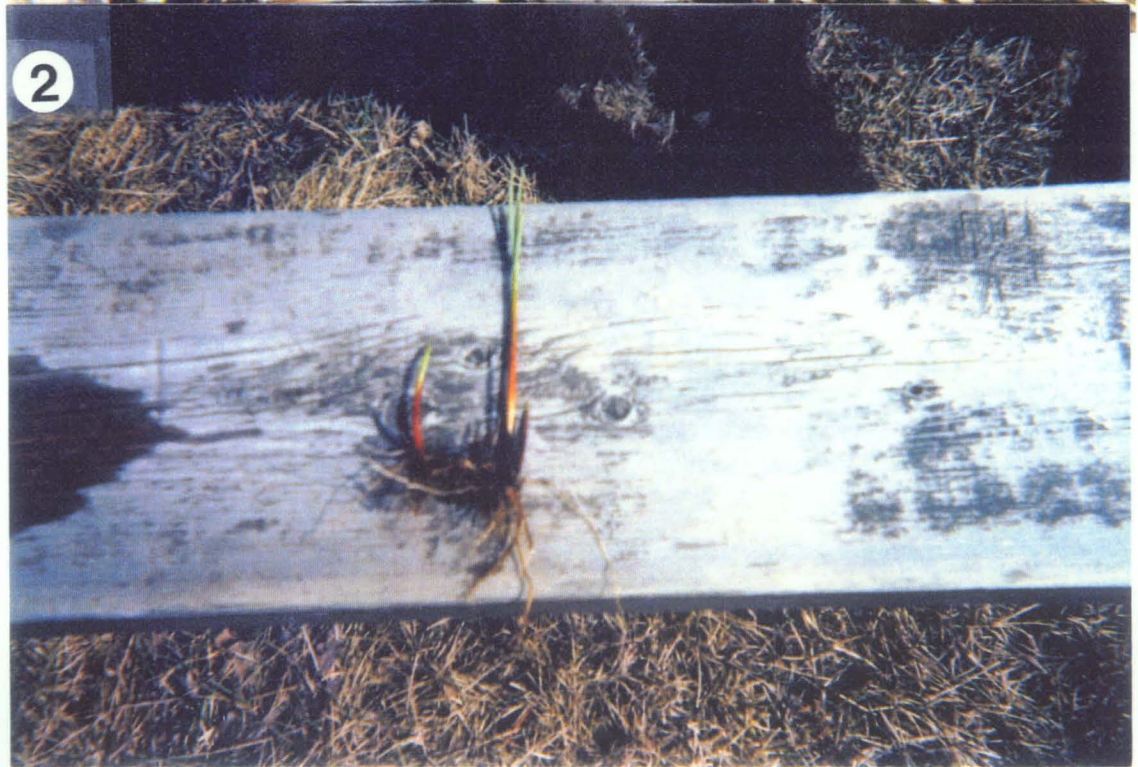


Figure 5.5 b (3) *Calamagrostis canadensis* shoots emerging from the meadow substrate in early May 1991 from below about 15 cm of water. (the marks on the pole are 10 cm apart). (4) A single individual removed from the soil. (the wood is ≈ 20 cm wide).



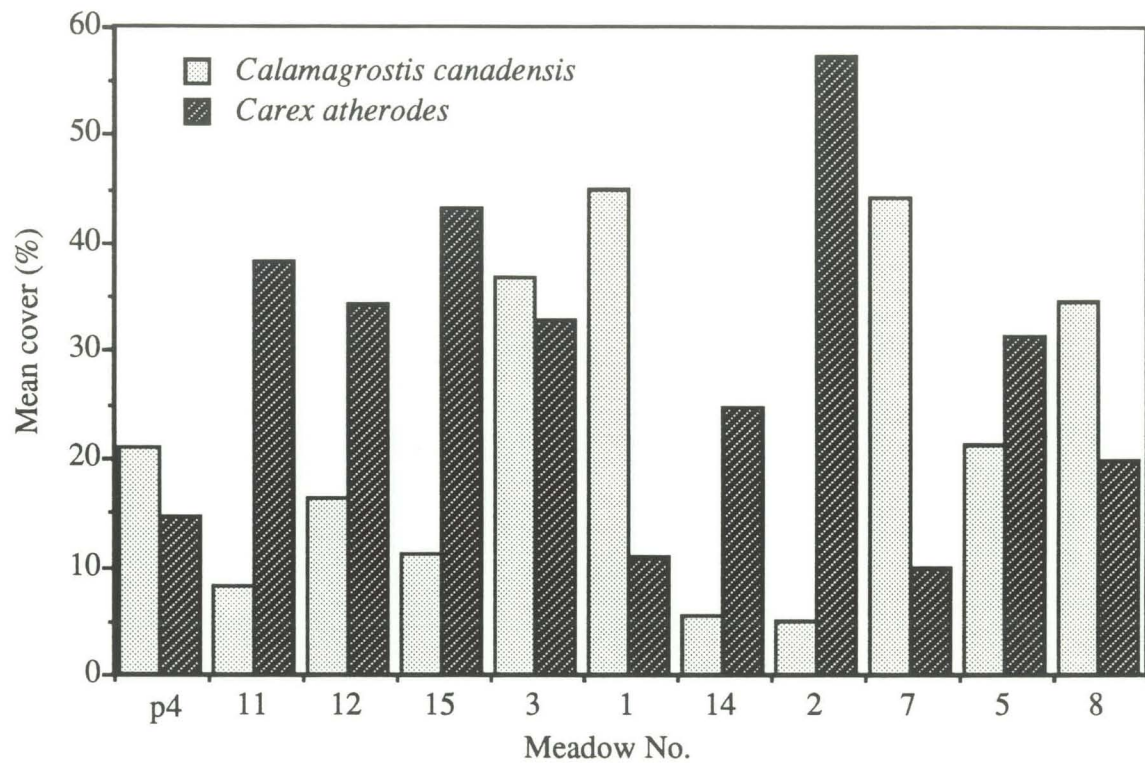


Figure 5.6 The mean percent cover of the two community dominants *C. atherodes* and *C. canadensis*. The meadows are ordered by age.

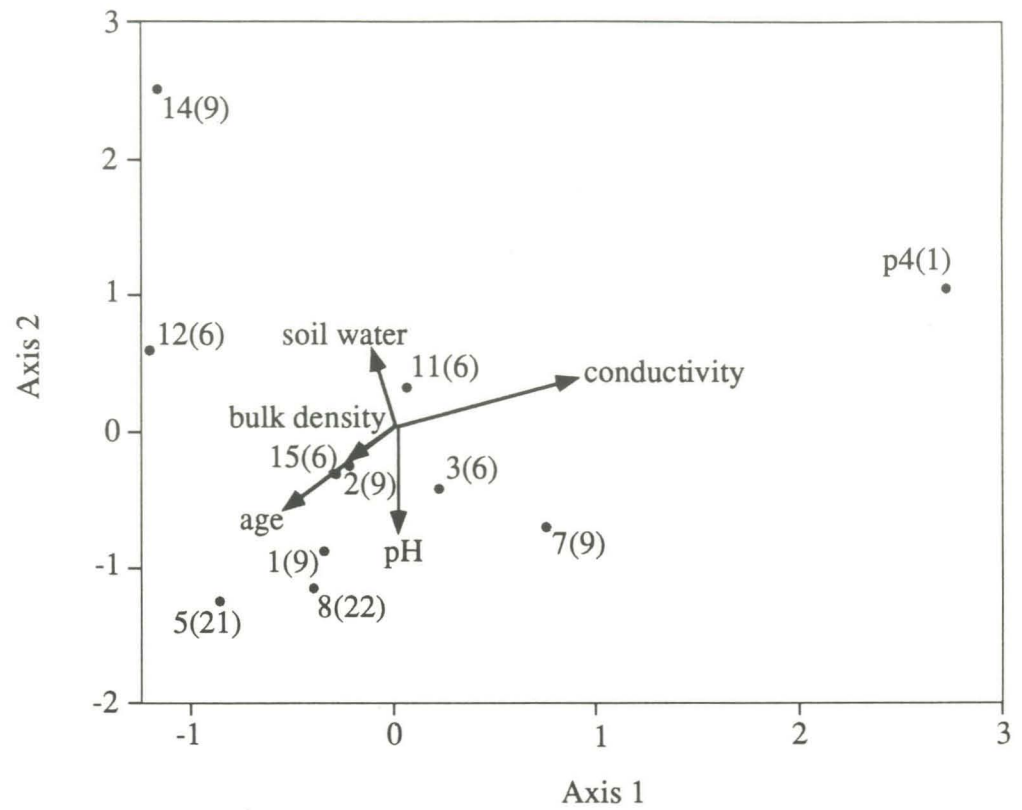


Figure 5.7 Canonical correspondence analysis of the beaver meadows, using all transects. The environmental variables used are pH, age, conductivity, bulk density, and soil water. The meadows are identified by number (age).

Table 5.7. Summary of the CCA eigenvalues for the analysis of transects one and two, transects three to five and all transects. A total of six environmental variables were used in the analysis: age of the meadow, soil water, soil pH, soil conductivity, bulk density of the soil, and organic content of the soil.

Axes	1	2	3	4	Total inertia
Ordination: Transects 1-2					
Eigenvalues	.255	.195	.147	.129	1.362
Species-environment correlations	.955	.967	.929	.962	
Cumulative percentage variance					
of species data	18.7	33.0	43.8	53.3	
of species-environment relation	28.5	50.4	66.8	81.3	
Ordination: Transects 3-5.					
Eigenvalues	.299	.169	.128	.101	1.277
Species-environment correlations	.979	.941	.977	.857	
Cumulative percentage variance					
of species data	23.4	36.6	46.7	54.6	
of species-environment relation	37.1	57.9	73.8	86.4	
Ordination: All transects					
Eigenvalues	.174	.161	.113	.069	1.036
Species-environment correlations	.918	.947	.961	.964	
Cumulative percentage variance					
of species data	16.8	32.3	43.2	49.9	
of species-environment relation	30.5	58.8	78.6	90.8	

years old) are at the opposite ends of the first axis. The canonical correlation results indicate that the first axis corresponds to meadow age and soil conductivity (which is highest in the one-year-old meadow). Species associated with the one-year-old meadow are generally annuals and short-lived, non-clonal perennials. These species are typically found colonizing mudflats and other open areas that are exposed after a dam is breached. The second ordination axis separates two of the meadows (meadow 12, 6 years old and meadow 14, 9 years old) from the others. These meadows have a higher soil moisture content and lower pH, and have relatively high abundances of the following species: *Agrostis scabra*, *Carex rostrata*, *Vicia americana*.

The ordination results indicate that the one-year-old meadow is floristically distinct, but that after approximately six years the meadow vegetation does not change appreciably with time. Indeed, there is as much vegetational variation between sites of the same age class (e.g., the 6 and 9 year old meadows) as there is between the age classes.

(b) Data from 'dam transects' (transects 1 and 2)

When the eleven meadows are compared based only on the vegetation of the dam tops and faces, similar results are obtained (Figure 5.8 and Table 5.7). Again, the first axis shows a weak age trend, serving mainly to distinguish the one-year-old meadow from the older ones. The one-year-old meadow site is again characterized by high soil conductivity, water content and organic matter content, and low soil bulk density. One of the six-year-old meadows (#15) is separated from the others along the second axis. The abandoned beaver dam is largely intact at this site, and the dam is parallel to a bend in the stream for most of its length. This particular dam face has a number of grass or rush species that are uncommon at the other sites, including *Beckmannia syzigachne*, *Glyceria striata*, *Scirpus* sp and *Phalaris arundinacea*. It was noted that these species are generally found only along the banks of the waterway.

(c) Data from 'meadow transects' (transects 3 to 5)

No age trends were seen when the eleven meadows were compared on the basis of vegetation composition of the meadow proper (transects 3-5) (Figure 5.9, Table 5.7). This is not unexpected, as it was noted that in the back reaches of beaver ponds emergent macrophyte species, such as *Carex atherodes* and *Calamagrostis canadensis* are able to persist at least in low to moderately flooded areas. The ordination results show that the 'back meadow' vegetation of the one-year-old site is in fact quite similar to that of the oldest

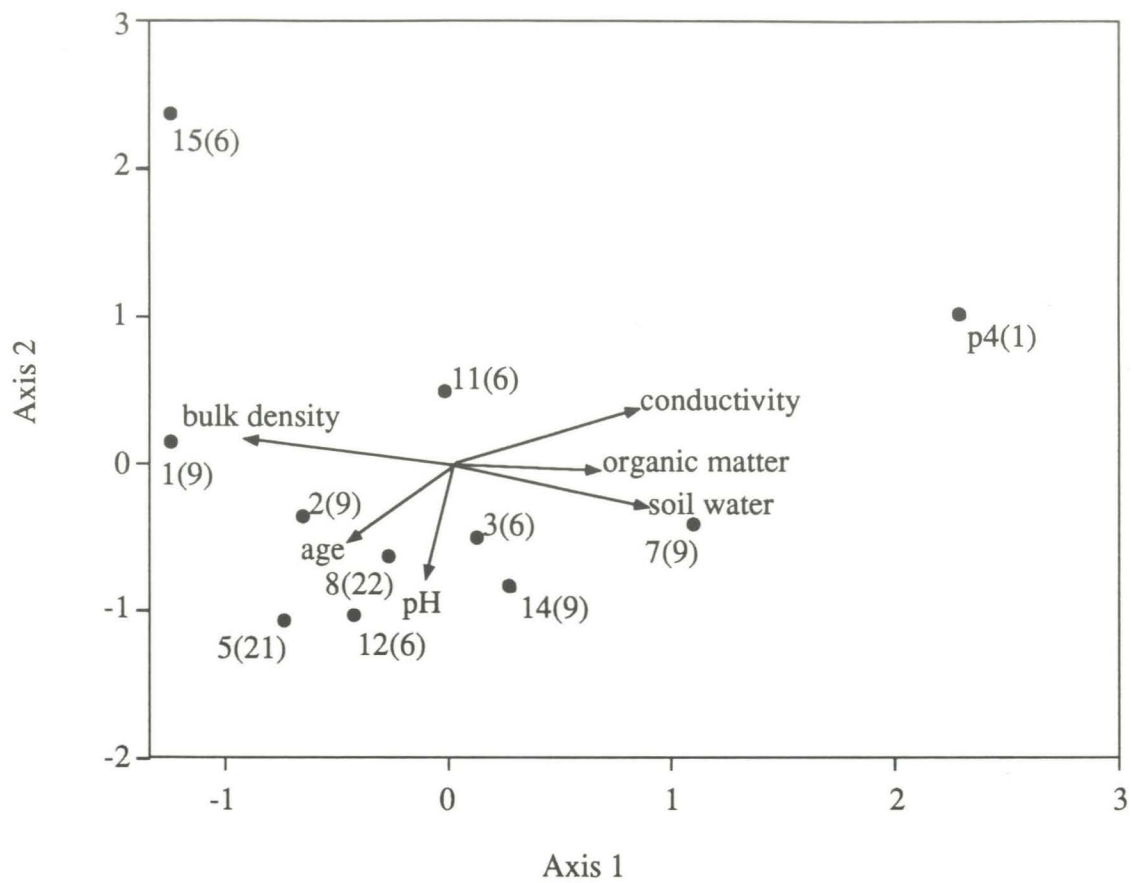


Figure 5.8 Canonical correspondence analysis ordination of the beaver meadows using dam top and dam face transects (transects 1-2). The environmental variables used are pH, age, conductivity, bulk density, organic matter, and soil water. Meadows are identified by number (age).

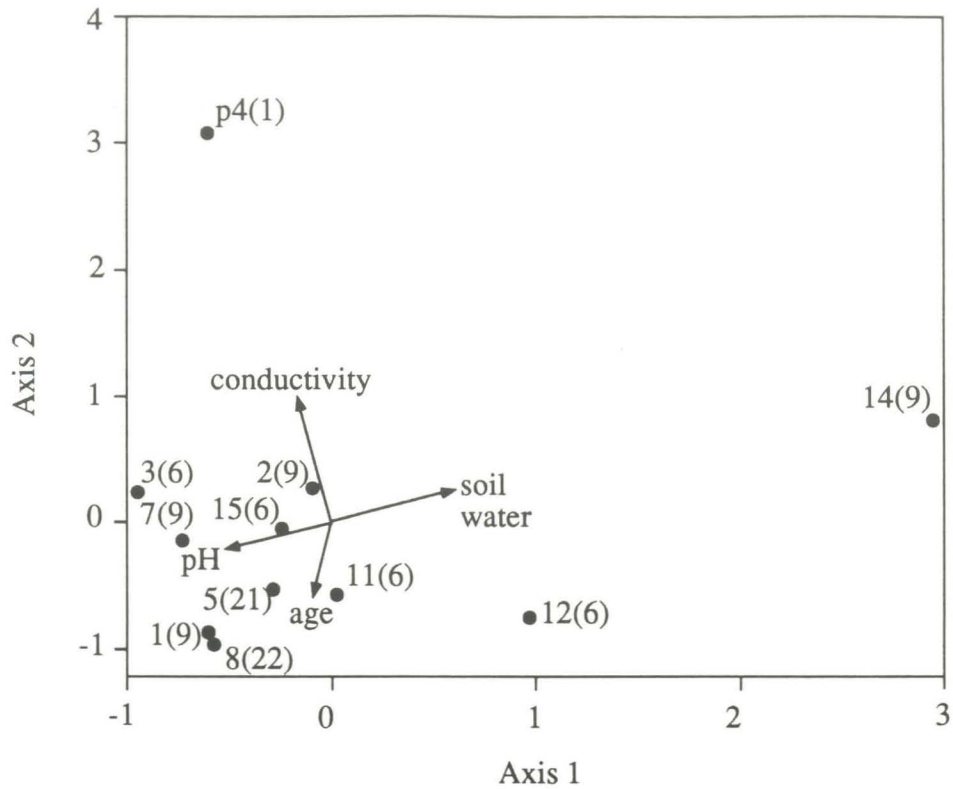


Figure 5.9 Canonical correspondence analysis of the beaver meadows using the main meadow transects (transects 3-5). The environmental variables used are pH, age, conductivity, and soil water. Meadows are identified by number (age). Bulk density and organic matter had very small environmental vectors and were therefore excluded from the graph.

meadows. It appears then that flooding by beaver dams has little effect on relatively flood tolerant macrophytes species such as *C. atherodes* and *C. canadensis*, at least up to certain water depths. Even if these species do die back, their rhizome system may survive flooding and allow them to re-establish at the site once the beaver dam is breached.

Shrub Composition

The shrub and tree species encountered in the meadows are listed in Table 5.4 and shrub density values in Table 5.8. Shrub density in the meadows showed a significant ($R^2 = 0.72$, $p < 0.01$) increase with increasing meadow age (Figure 5.10), suggesting that shrub invasion of grass-sedge meadows does occur. However, shrub/tree densities remained relatively low even in the oldest meadows. None of the individuals exceeded 2 m in height. Most shrubs were found along the periphery of the former ponds, in areas of higher elevation (Figure 5.11).

This suggests that annual spring flooding may preclude the establishment of shrubs in wetter regions of the watercourse. Heavy browsing by moose, and in some cases beaver activity, was also noted. Annual flooding together with heavy browsing may prevent shrubs from invading meadow sites to any extent.

Table 5.8. Shrub and tree densities in the meadows.

Meadow	Meadow Age	Density (No./ha)	No. Species	No. Quadrats
Pond 4	1	0.00	0	9
15	6	17.48	4	20
3	6	26.22	4	8
11	6	34.97	4	7
12	6	69.93	4	5
14	9	19.43	2	12
2	9	25.07	2	28
1	9	27.55	3	19
7	9	31.38	5	13
5	21	83.92	4	10
8	22	154.43	3	24
Total			11	155

Relationship between the extant vegetation and the seed bank:

Percent similarity values relating seed bank composition to the extant vegetation were low for all meadows, indicating a weak relationship between the two (Table 5.9 a). The seed bank was dominated by weedy annuals and short-lived perennials, whereas the extant vegetation was dominated by long-lived, clonal perennials such as *Carex atherodes* and *Calamagrostis canadensis*. Percent similarity between extant vegetation and the seed bank was greatest for the younger meadows (Table 5.9 b). This indicates a greater abundance of weedy annuals and short-lived perennials in the extant vegetation of the younger meadows.

Table 5.9a Similarity (%) between the extant vegetation and the seed bank for the cold treated and the non- cold treated soil samples.

Meadow	Age (yrs)	Similarity (non cold)	Similarity (cold)
p4	1	0.2520	0.1911
3	6	0.0495	0.1108
11	6	0.2242	0.1742
12	6	0.1466	0.0761
15	6	0.1140	0.0558
1	9	0.1362	0.0602
2	9	0.1551	0.1061
7	9	0.0909	0.1212
14	9	0.1512	0.1576
5	21	0.1671	0.0714
8	22	0.0716	0.0249

Table 5.9b Similarity (%) between the extant vegetation and the seed bank for the cold treated and the non- cold treated soil samples averaged by age.

Age (yrs)	Similarity (non cold)	Similarity (cold)
1	0.252	0.191
6	0.133	0.104
9	0.133	0.111
21 - 22	0.119	0.048

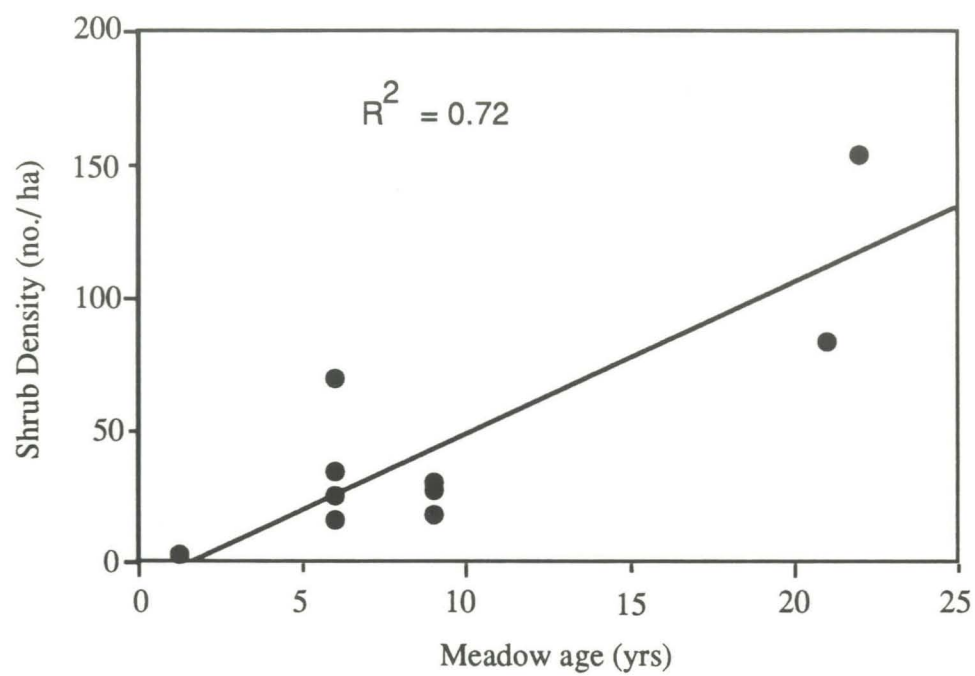


Figure 5.10. Changes in shrub species density with age. Each point is the average shrub density in the meadows of the eleven drained ponds.

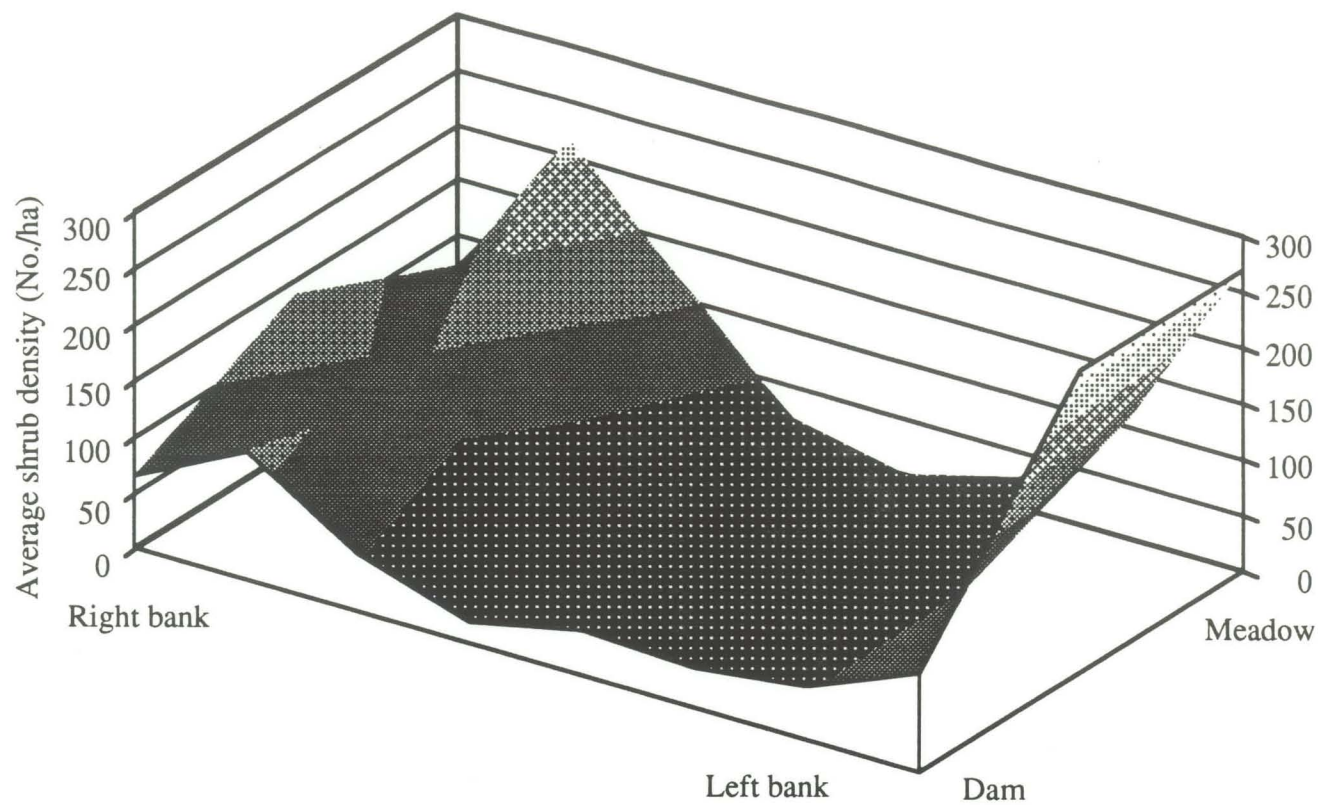


Figure 5.11. Shrub density change with location within all the meadows. This is the average shrub density by location for all meadows

5.4 Discussion

Vegetation-Age Gradients

The results suggest that there is some change in vegetation following the breaching of a beaver dam. However, the rate of vegetation change appears to be greatest at the early stages (that is, immediately following dam breaching), and by the sixth year little change in the vegetation is observed over time. After a dam is breached, mudflats are exposed which are colonized by annuals and short-lived perennials from the seed bank. This community apparently does not persist for long, since by year six cover of annual plants in the meadows drops dramatically while the cover of the community dominants (particularly the sedge *Carex athodes* and the grass *Calamagrostis canadensis*) increases. I hypothesize that as the meadow ages, the mudflats are invaded by a denser vegetation consisting of long-lived, clonal and flood-resistant species that out compete the early colonizers. Although annual plant species such as *Mentha arvensis* and *Bidens cernua* are uncommon in older meadows, they are able to persist along the watercourse due to the disturbance of the ecosystem by beaver damming. The beaver populations thus play an important role in promoting and maintaining high plant species richness along the Little Saskatchewan River valley.

Shrub Invasion

The results also indicate an increase in shrub density with increasing meadow age. However, even in the oldest meadows shrub density remained relatively low, and individuals were restricted to higher elevations along the periphery of the meadow. This observation suggests that shrub establishment in the meadow is prevented by periodic

flooding. In some years (e.g., the spring of 1992), very high water levels (enough to cover most of the river valley in water) persist for a considerable period of time. The relative flood-intolerance of most trees and shrubs may preclude their establishment and/or persistence in the wetter parts of the meadow.

Previous studies (eg. Naiman 1988) have suggested that beaver meadows continue to gradually fill in with shrubs and trees until the site is again flooded by the building of a beaver dam. This does not appear to be occurring along the Little Saskatchewan River system, however, as low shrub density was observed in even the oldest meadows. As already mentioned, this may be due to periodic spring flooding of the valley. Alternatively, heavy browsing by beaver of shrubs along the watercourse may keep shrub densities low. More studies are required to determine what factors are most important in preventing shrub establishment along the watercourse.

Vegetation-Seed Bank Relationships:

My results indicate a low degree of similarity between the seed bank composition and the extant vegetation. This has been found for other inland wetlands, including prairie marshes (van der Valk & Davis 1978) and lakeshores (Keddy & Reznicek 1982). The seed bank is dominated by annuals and short-lived perennial species that are relatively poor competitors. Most of these are ruderal species (sensu Grime 1979) which establish on exposed mudflats and persist in the seed bank. The extant vegetation of older meadows is dominated by long-lived clonal perennials such as *Carex atherodes* and *Calamagrostis canadensis*, which are strong competitors. These species may colonize the mudflats over time through seed germination or vegetative propagation.

Evidence from my study suggests that the seed bank is important in the initial colonization of mudflats. Newly exposed mudflats had a flora dominated by annual species that were also dominant in the seed bank (see Table 5.6). Further, the mean percent similarity between the seed bank and the extant vegetation was higher for the one year old meadow (25%) than for the older meadows (range of 12-14%). This result supports the idea that the seed bank plays a role in determining the vegetation of beaver meadows immediately following a dam breach. However, by the sixth year there is little correspondence between the vegetation and the seed bank flora. This indicates that the species dominating the extant vegetation are not the primary contributors to the seed bank. It seems likely that the seed bank is instead derived from the seed rain of plant species that are located further upstream on exposed mudflat 'islands'. Seeds of these ruderal species may persist in the soil bank for extended periods of time.

Evidence of the superior competitive ability of the community dominants *Carex atherodes* and *Calamagrostis canadensis* is somewhat circumstantial but nonetheless convincing. Both species are strongly clonal and apparently well adapted to growing on periodically flooded substrates. In early May of 1992, both of these species were observed sporting new vegetative shoots through 15 cm of water (see Figure 5.4). Their ability to begin growth early in the spring, and their strong clonal habit and ability to form dense monodominant stands, suggests that they are strong competitors in periodically flooded areas. Their dominance along the meadow system of the Little Saskatchewan River is broken (temporarily) only when they are killed by flooding from beaver dam construction.

5.5 Summary

1. Newly drained meadows (one-year-old) have a distinctive flora dominated by annuals and short-lived perennials which establish on exposed mudflats following drainage. These areas are generally found near the base of the dam where the water was deepest and the emergent macrophyte vegetation was killed. By six years, these areas have largely disappeared to be 'taken over' by the community dominants.
2. Major community dominants do not show a change in abundance with meadow age, suggesting that they are able to persist even with flooding. Structurally, the meadow communities display little variation with age (with the exception of the exposed mudflat areas discussed above).
3. The two community dominants *Carex atherodes* and *Calamagrostis canadensis* show vary in abundance between the meadows, and by meadow age. Which species dominates a given meadow may be largely attributable to chance; the species that arrives first at the site continues to dominate. Both species are strongly clonal and form dense, monodominant stands that preclude the establishment of the other species.
4. The meadows are floristically similar, with the same dominant species occurring throughout. Less common species are generally found in small patches within the meadow at high local abundance. Amongst the uniformity of the dominant vegetation would be found small patches of unique species combinations, locally abundant but overall rare in the meadow as a whole. These patches (floristic 'islands') were characteristic of the following areas: (a) dam top of newly abandoned meadows; (b) exposed mudflats following pond drainage; (c) riverbank communities; (d) local

disturbance sites in the meadow (e.g., trampling by large mammals); (e) areas adjacent to the riverbed that appear to be subjected to scouring during spring runoff; (f) areas where the soil is very high in organic content; (g) areas where the soil has very high inorganic content.

5. Shrub density increases with increasing meadow age. However, shrub establishment is restricted to higher and drier areas of the former pond periphery. Shrubs appear to be precluded from establishing in the wet meadow by spring flooding (personal observation). Herbivory and beaver activity may also have an effect in preventing the development of dense shrub and tree stands in the meadow and along its periphery. Increasing shrub density over time indicates that the meadows become drier over time. This is likely attributable to the continued erosion of the dam over time. As further erosion takes place, less water is held back in the spring freshet and less of the meadow is flooded. This allows shrub establishment on higher ground.
6. The correspondence between the seed bank and the extant vegetation is quite low for all meadow ages. Generally, the seed bank is dominated by annuals and short-lived perennials ('weedy' species) while the extant vegetation of all meadows is dominated by the clonal emergent macrophytes *Carex atherodes* and *Calamagrostis canadensis*. The similarity between extant vegetation and seed bank is greatest for the younger meadows, reflecting the greater abundance of annuals and short-lived perennials in the extant vegetation (which of course germinated from the soil seed bank).
7. These results suggest that the vegetation of meadows along the Little Saskatchewan River system is determined in large part by flooding, at two levels. The first, related to the annual cycles of spring flooding, appears to be important in maintaining these sites in a meadow state (that is, allowing dense monodominant stands of *Calamagrostis canadensis*

and *Carex atherodes* to establish and persist over extended periods of time), and precluding the establishment of dense shrub stands, and tree species, in these areas. The second is beaver activity. The building and maintenance of a beaver dam floods an extensive area, but in the shallower waters the community dominants are able to persist (though at lower densities, personal observation). Vegetation is killed in the deepest areas of the pond, however. When the pond drains, these exposed mudflats are colonized by annual and short-lived perennial species present in the seed bank. These floristic 'islands' persist for only short periods (six year old meadows show little evidence of these islands), but are apparently frequent enough in occurrence to allow these species to continue to be present in the seed bank, 'waiting' for the next disturbance event. This has analogies with the work of van der Valk in prairie marsh vegetation (1981). These two flooding factors operate at different spatio-temporal scales. Annual flooding events allow the dominant meadow vegetation to establish and perpetuate itself along the entire river system for very extended periods of time. Beaver activity operates at more local spatial scales and for shorter periods of time, serving mainly to temporarily remove the community dominants from small mosaic patches (mudflats) within the sea of dominant vegetation. Other disturbance factors such as riverbank scouring, herbivore trampling, and buildup of organic debris may have an analogous effect.

Chapter 6 Summary

1. Newly drained beaver meadows have a distinctive flora, dominated by annuals and short-lived perennials, that establishes on exposed mudflats following drainage. These mudflats are generally found near the base of the dam, in areas where the water was sufficiently deep to kill the emergent macrophyte species. The soils of newly drained meadows are higher in conductivity, soil moisture, and organic matter, and lower in bulk density, than the soils of older meadows. By the sixth year, areas dominated by annuals and short-lived perennials have largely disappeared, having been replaced by the community dominants *Carex atherodes* and *Calamagrostis canadensis*.
2. The two community dominants, *Carex atherodes* and *Calamagrostis canadensis*, vary in abundance between the meadows, and with meadow age. Which species dominates a given meadow may be determined largely by chance; specifically, the species that first arrives at a given location may come to dominate that space for long periods of time. Both *C. atherodes* and *C. canadensis* are strongly clonal, forming dense monodominant stands that may preclude the establishment of other species. Once established, these species perpetuate at a site by strong vegetative propagation, which prevents the establishment of other species. There is some evidence of increasing dominance by *C. canadensis* in the older meadows, but a more detailed study would be required to determine whether this reflects the superior competitive ability of the species, or changing environmental conditions.
3. Dominance of *C. atherodes* and *C. canadensis* may reflect their ability to persist in low to moderately flooded areas. Indeed, flooding by beaver dams appeared to have little effect on these species, at least up to certain water depths. Even if they do die back, their

rhizome system may survive flooding and therefore allow them to re-establish at the site once the beaver dam is breached.

4. With the notable exception of newly-formed (one-year-old) meadows, the beaver meadows are floristically similar and have the same two dominant species occurring throughout. Less common species are generally found at high local abundance within small patches in the meadows. These patches, or floristic 'islands', are characteristic of the following areas: (a) dam top of newly abandoned meadows; (b) exposed mudflats following pond drainage; (c) riverbank communities; (d) local disturbance sites in the meadow (e.g., trampling by large mammals); (e) areas adjacent to the riverbed that appear to be subjected to scouring during spring runoff; (f) areas where the soil is very high in organic content; (g) areas where the soil has very high inorganic content.
5. Shrub density increases with increasing meadow age. However, shrub establishment is restricted to higher and drier areas (i.e. the former pond's periphery). Shrubs appear to be precluded from establishing in the wet meadow by spring flooding. Herbivory and beaver activity may also serve to prevent the development of dense shrub and tree stands in the meadow and along its periphery. The observed increase in shrub density over time likely indicates that meadows become drier over time. This may reflect the erosion of the dam over time, resulting in less water being held back during the spring freshet.
6. The correspondence between the seed bank and the extant vegetation is quite low for all meadow ages. The seed bank is dominated by ruderal species (annuals and short-lived perennials), while the extant vegetation of all meadows is dominated by clonal emergent macrophytes (particularly *Carex atherodes* and *Calamagrostis canadensis*). The similarity between extant vegetation and seed bank is greatest for the younger meadows, reflecting the high abundance of recently-germinated species on the newly exposed mudflats.

7. The vegetation of beaver meadows along the upper Little Saskatchewan River is determined in large part by flooding, at two levels (Figure 6.1). The first level is related to the annual cycles of spring flooding, and is important in maintaining these sites in a 'meadow state'. Annual flooding cycles allow for the establishment and perpetuation of dense monodominant stands of *Calamagrostis canadensis* and *Carex atherodes*, while at the same time precluding the establishment of flood-intolerant shrub and tree species. The second level is related to beaver activity. The building of a beaver dam results in the flooding an extensive areas. Emergent vegetation is killed in the deepest areas of the pond, but in shallower water the community dominants are able to persist (though at lower densities). These two flooding factors operate at different spatio-temporal scales. Annual flooding events allow the dominant meadow vegetation to establish and perpetuate itself along the entire river system, for extended periods of time. Beaver activity operates at more local spatial scales and for shorter periods of time, serving mainly to temporarily remove the community dominants from small mosaic patches (mudflats) within the 'sea' of dominant vegetation.

8. When a pond drains, the exposed mudflats are colonized by annual and short-lived perennial species that are present in the seed bank. These floristic 'islands' persist for only short periods of time, but exposed mudflats appear frequent enough in the area to allow the ruderal species associated with these habitats to persist. These species are present in the seed bank, awaiting the next disturbance event. This has analogies with van der Valk's (1981) model of prairie marsh vegetation, and is consistent with the intermediate disturbance hypothesis (which states that species richness is promoted by not-to-frequent habitat disturbances). Specifically, the formation and subsequent breaching of the beaver dams is a disturbance that serves to maintain high species diversity within the beaver meadow complex.

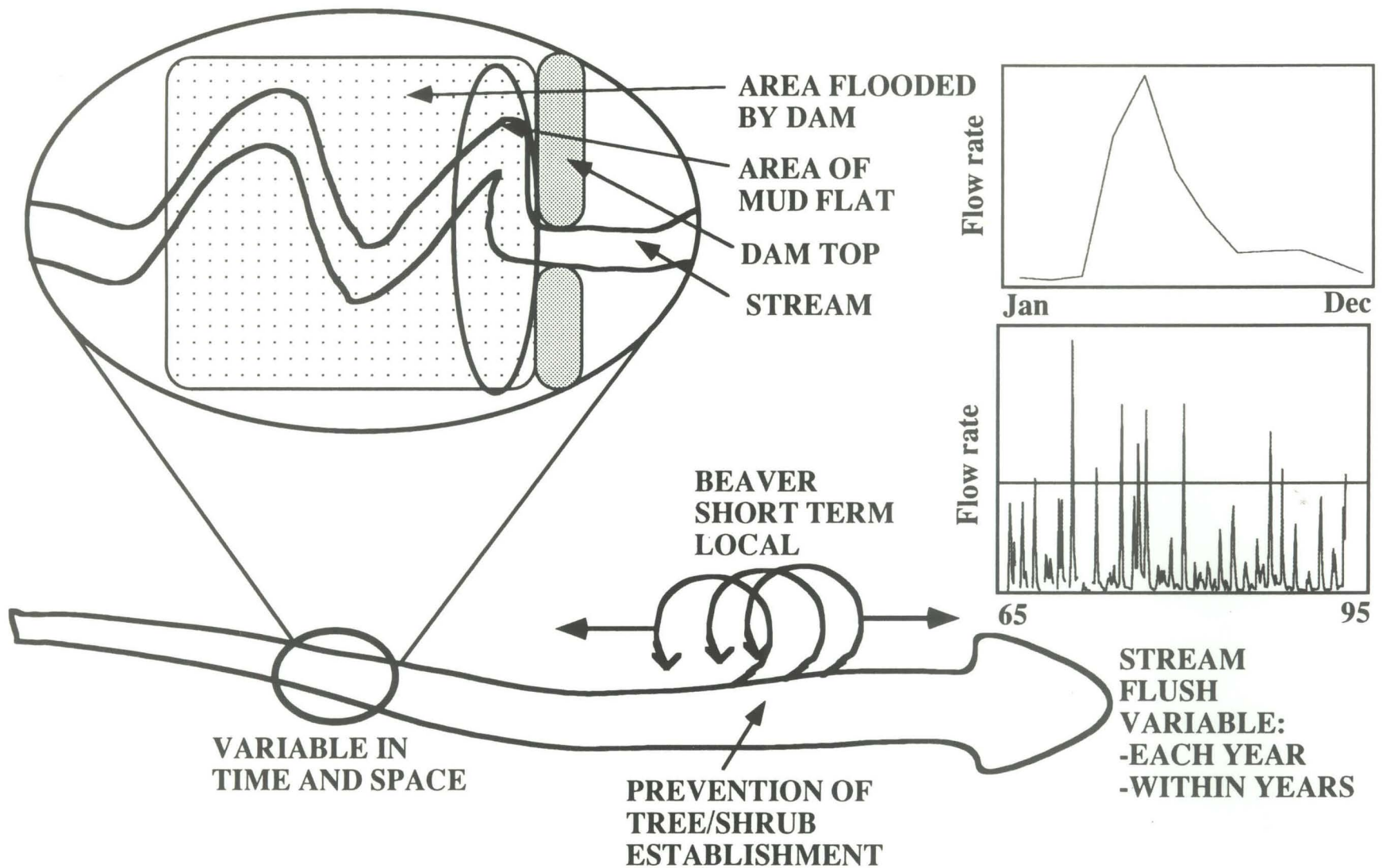


Figure 6.1 The two levels of flooding at work in a boreal stream system. The first is related to periodic whole-valley flooding of the river. The second is related to local flooding attributable to beaver activity.

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Appendices

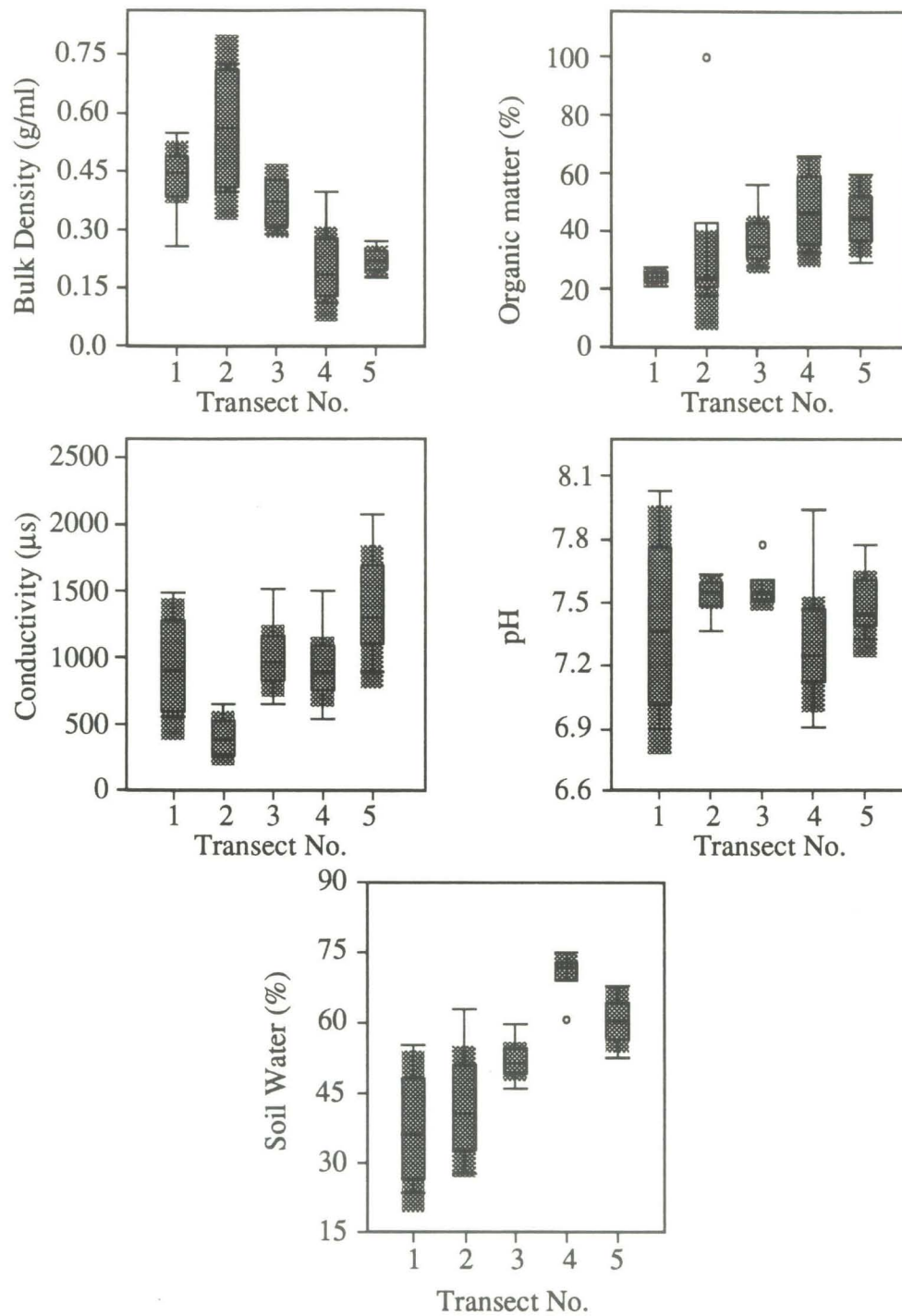


Figure A 1.1 Boxplots of within-meadow variation in soil factors, meadow 1.

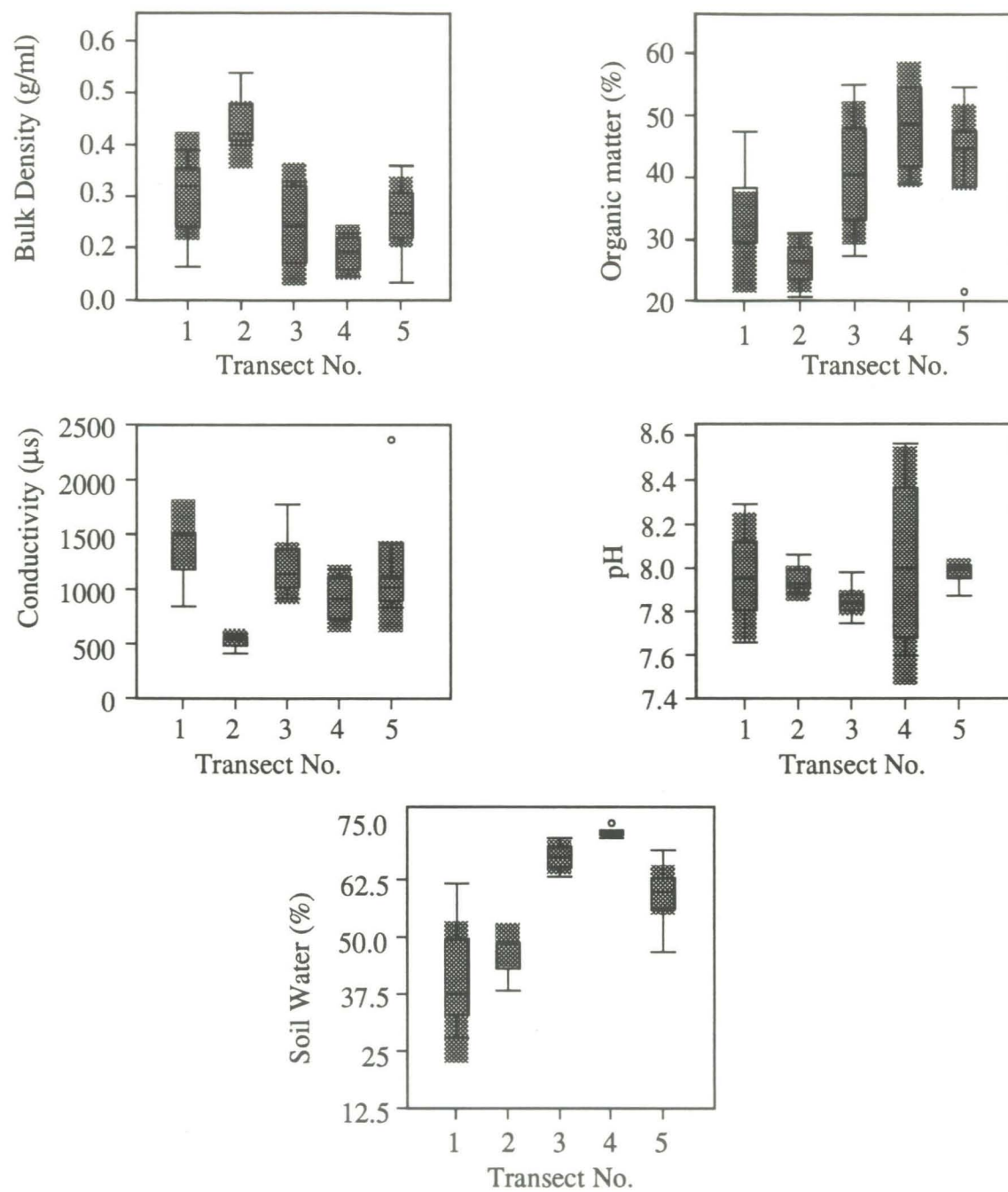


Figure A 1.2 Boxplots of within-meadow variation in soil factors, meadow 2.

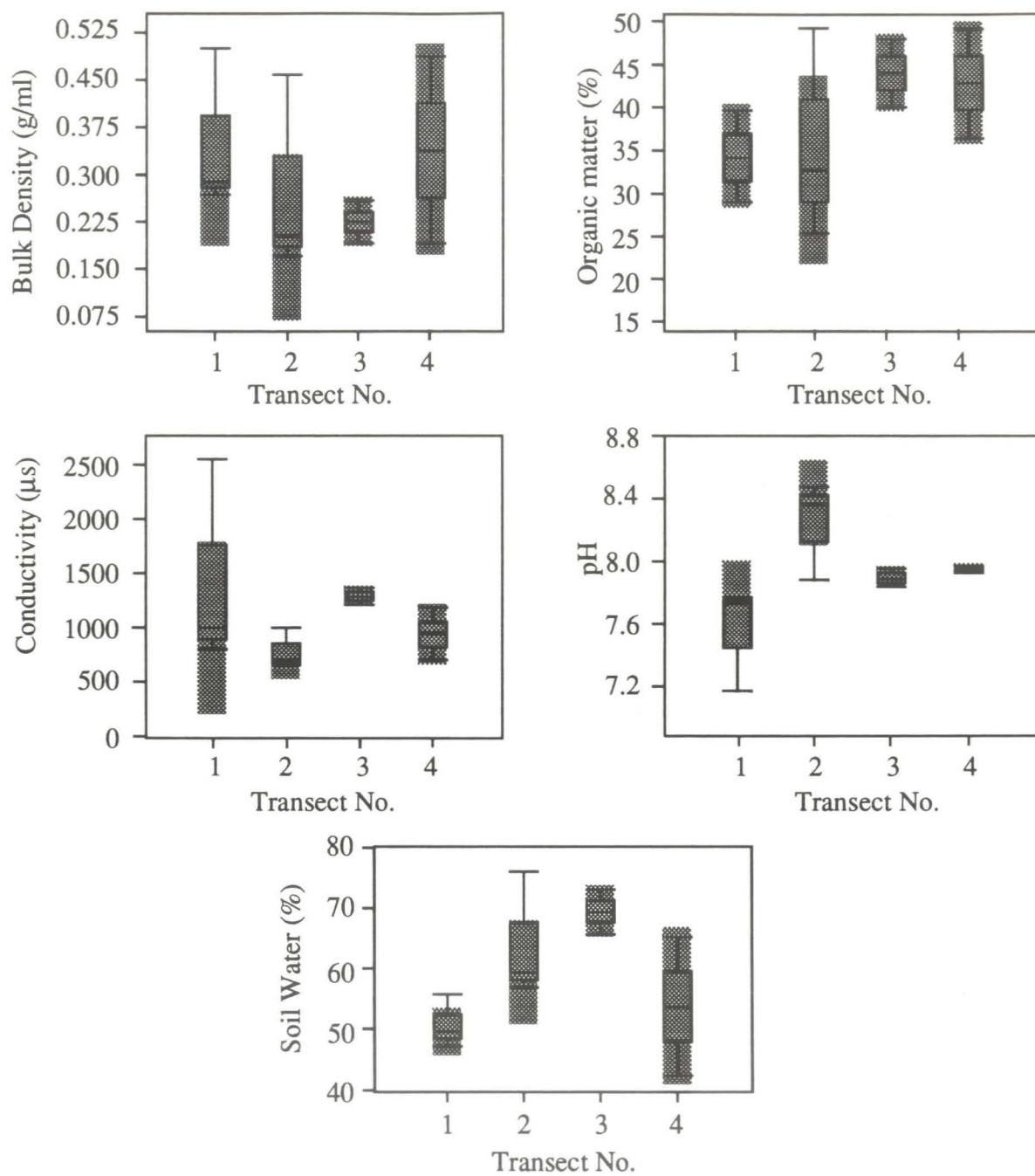


Figure A 1.3 Boxplots of within-meadow variation in soil factors, meadow 3.

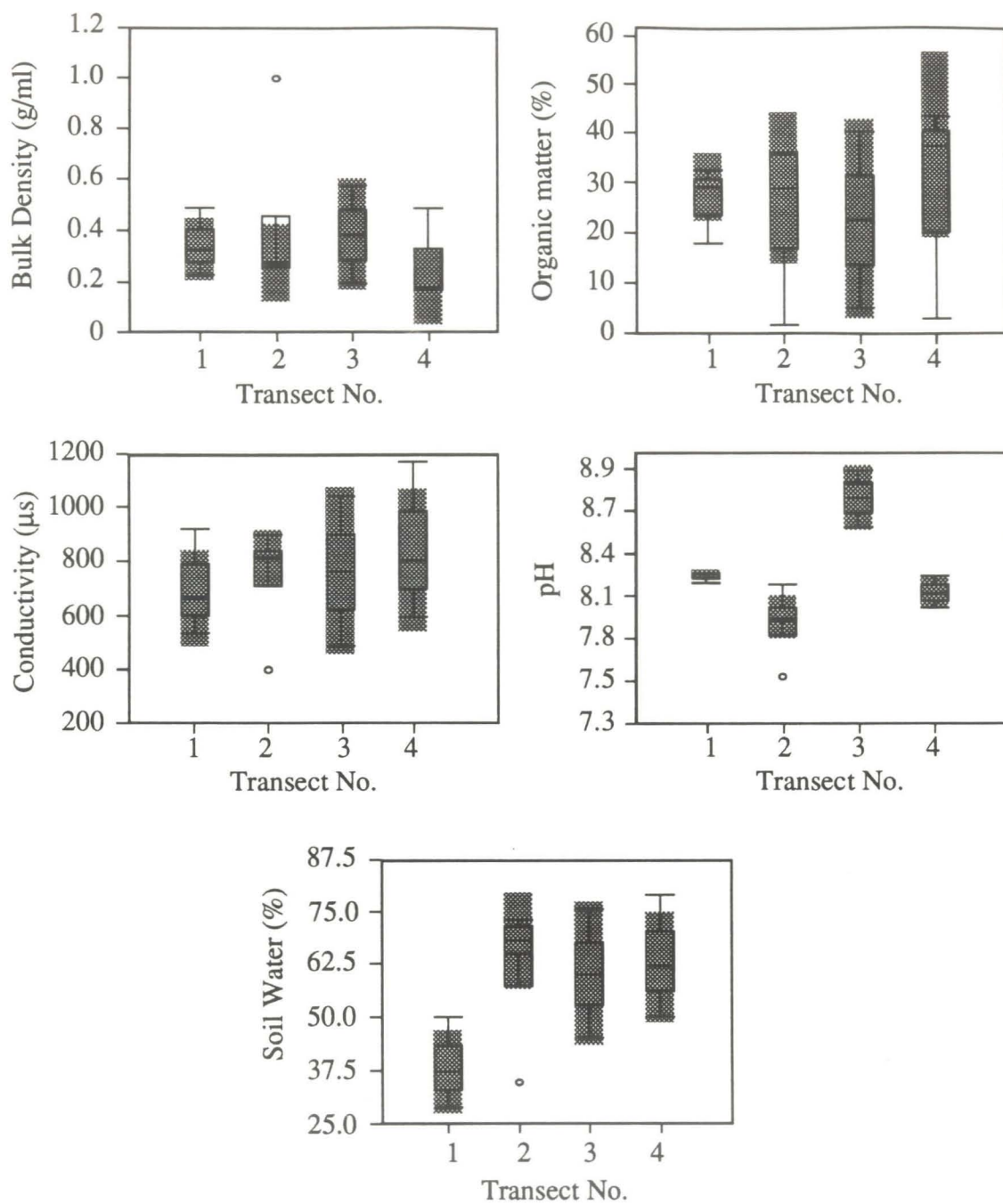


Figure A 1.4 Boxplots of within-meadow variation in soil factors, meadow 5.

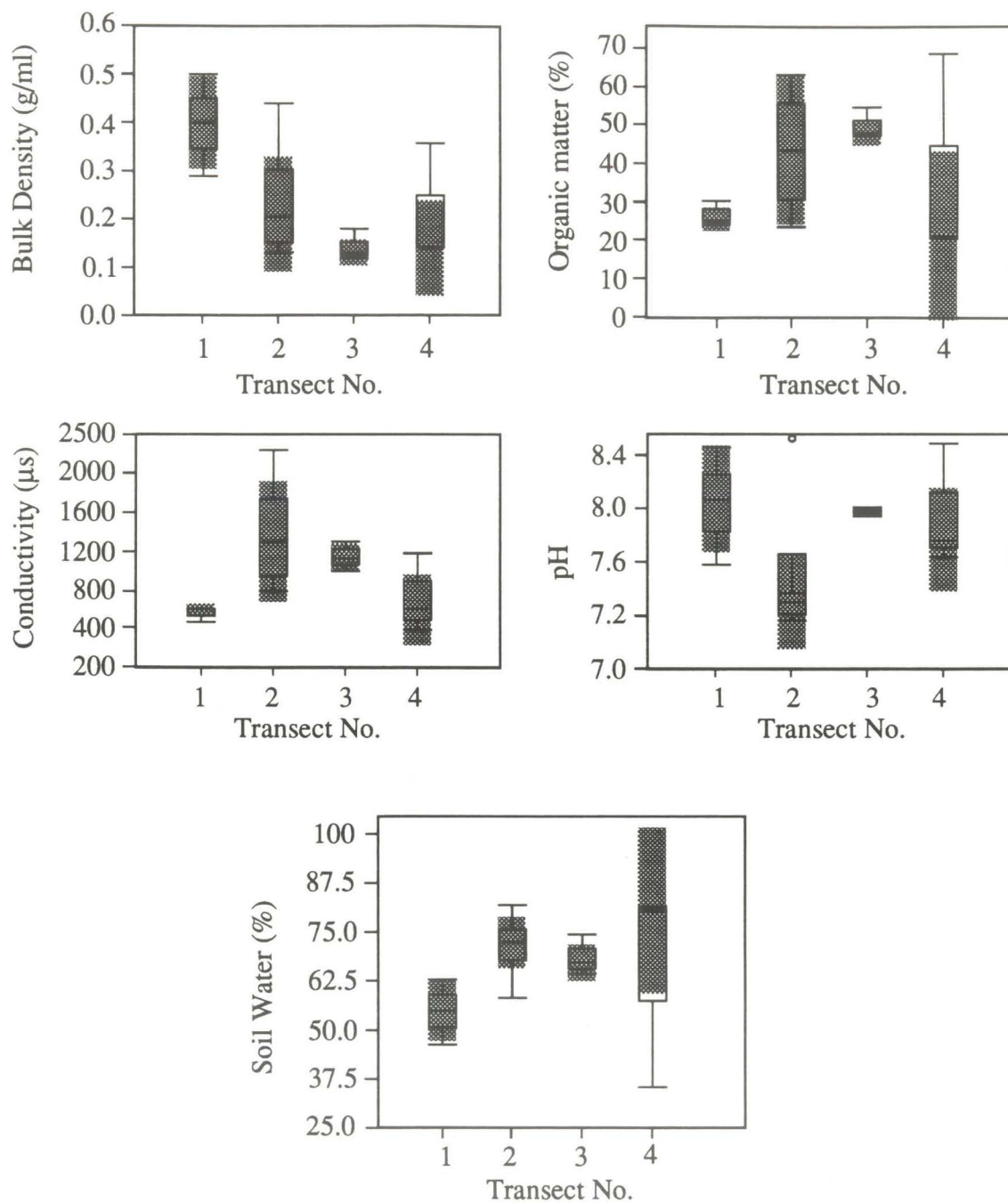


Figure A 1.5 Boxplots of within-meadow variation in soil factors, meadow 7.

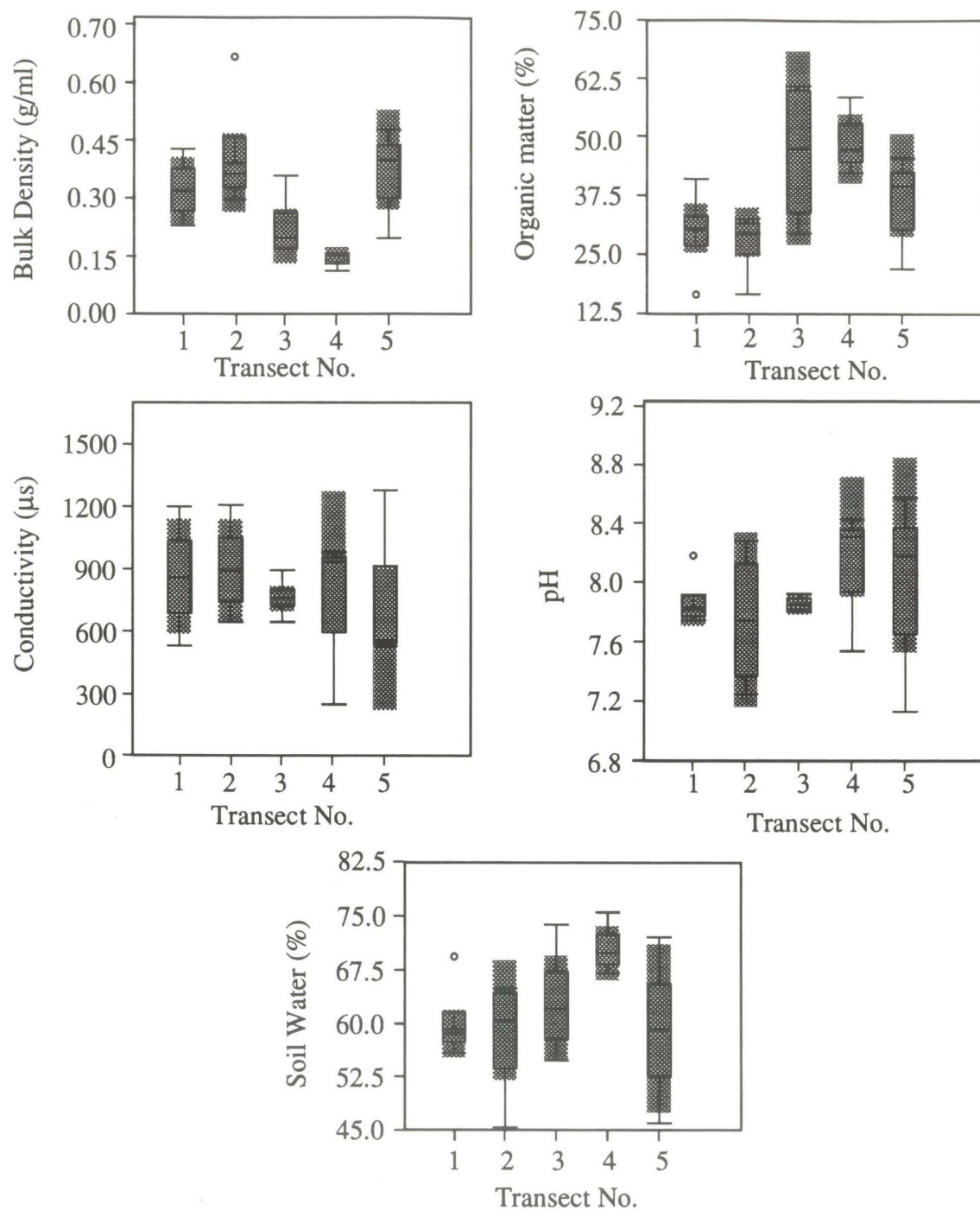


Figure A 1.6 Boxplots of within-meadow variation in soil factors, meadow 8.

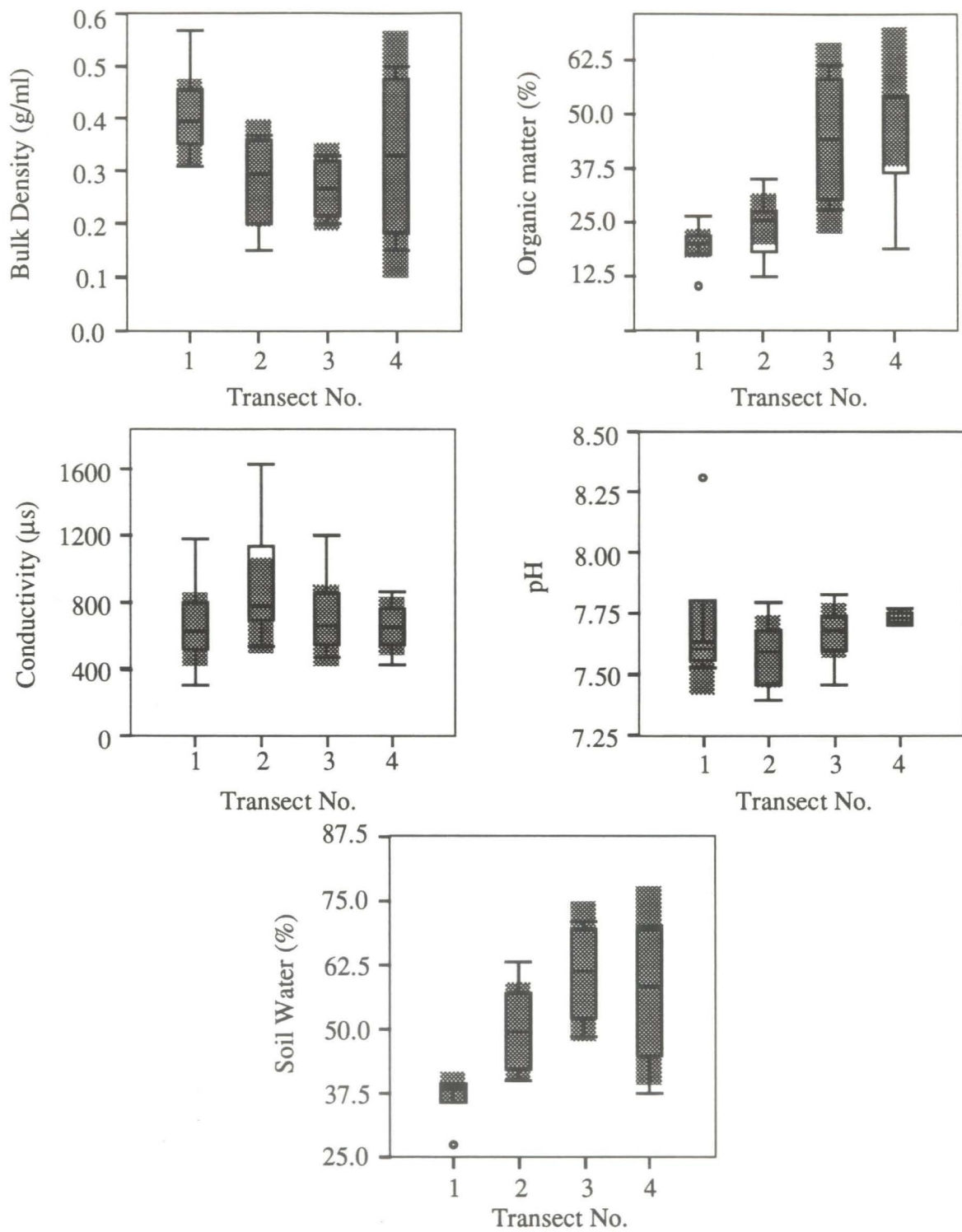


Figure A 1.7 Boxplots of within-meadow variation in soil factors, meadow 11.

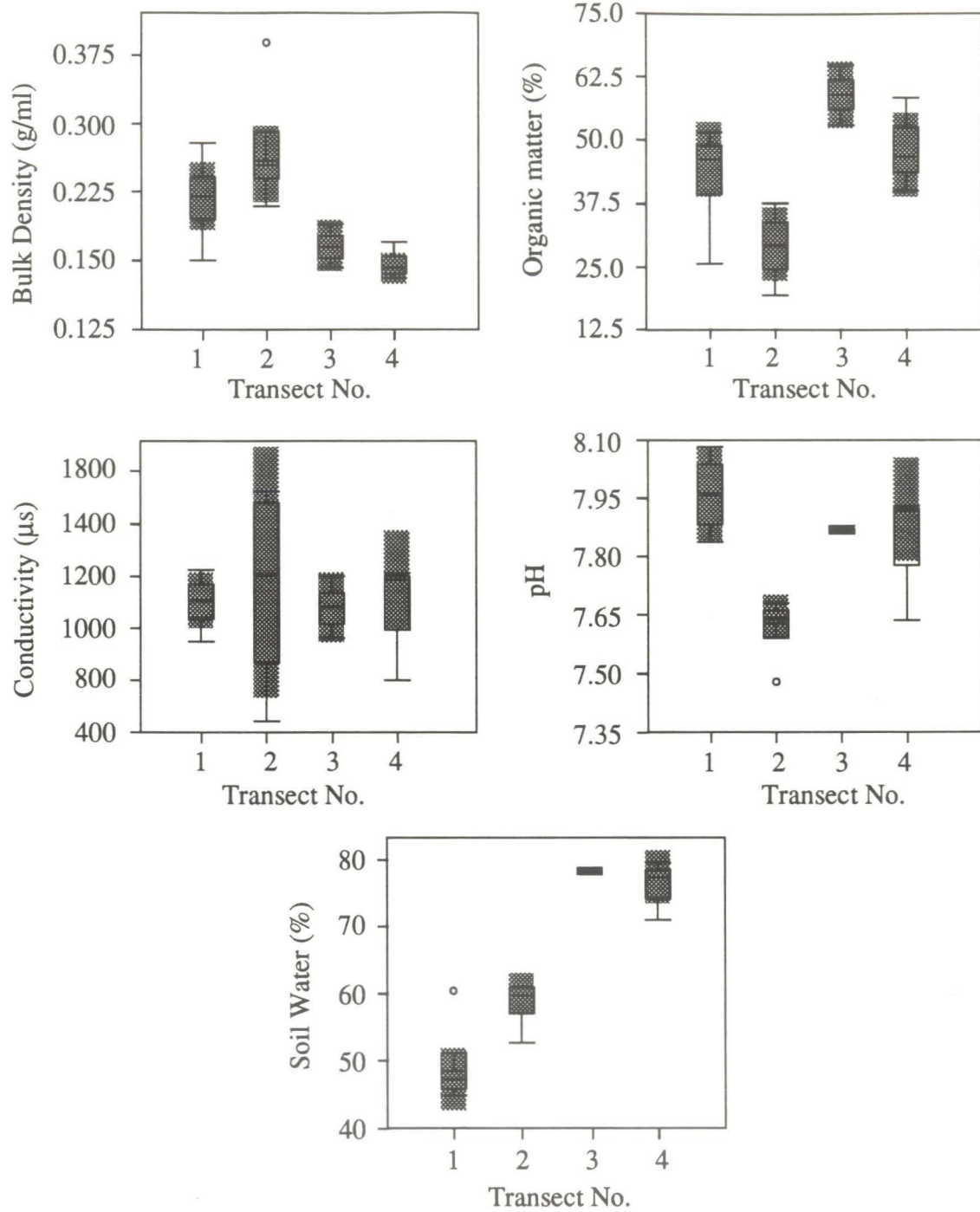


Figure A 1.8 Boxplots of within-meadow variation in soil factors, meadow 12.

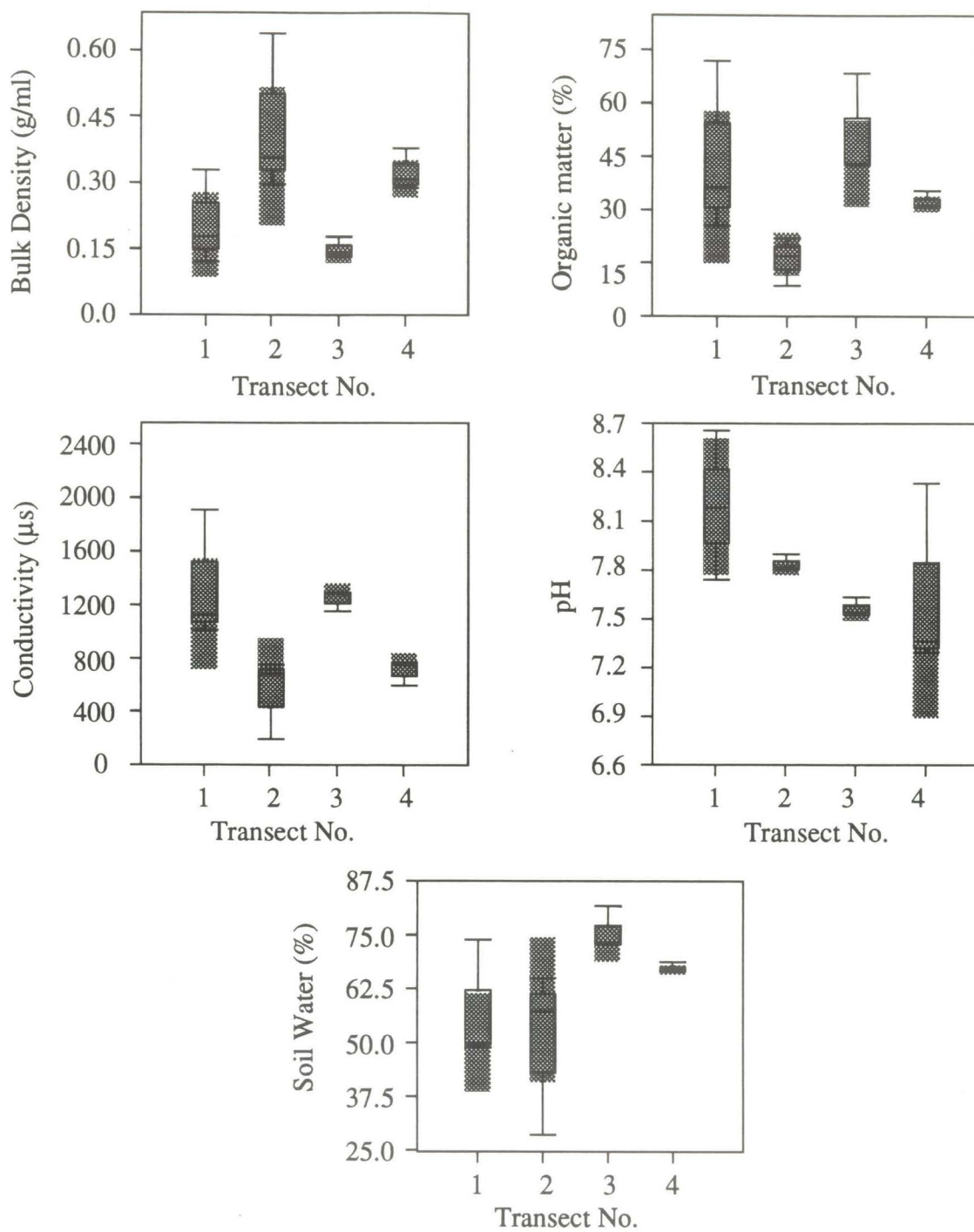


Figure A 1.9 Boxplots of within-meadow variation in soil factors, meadow 14.

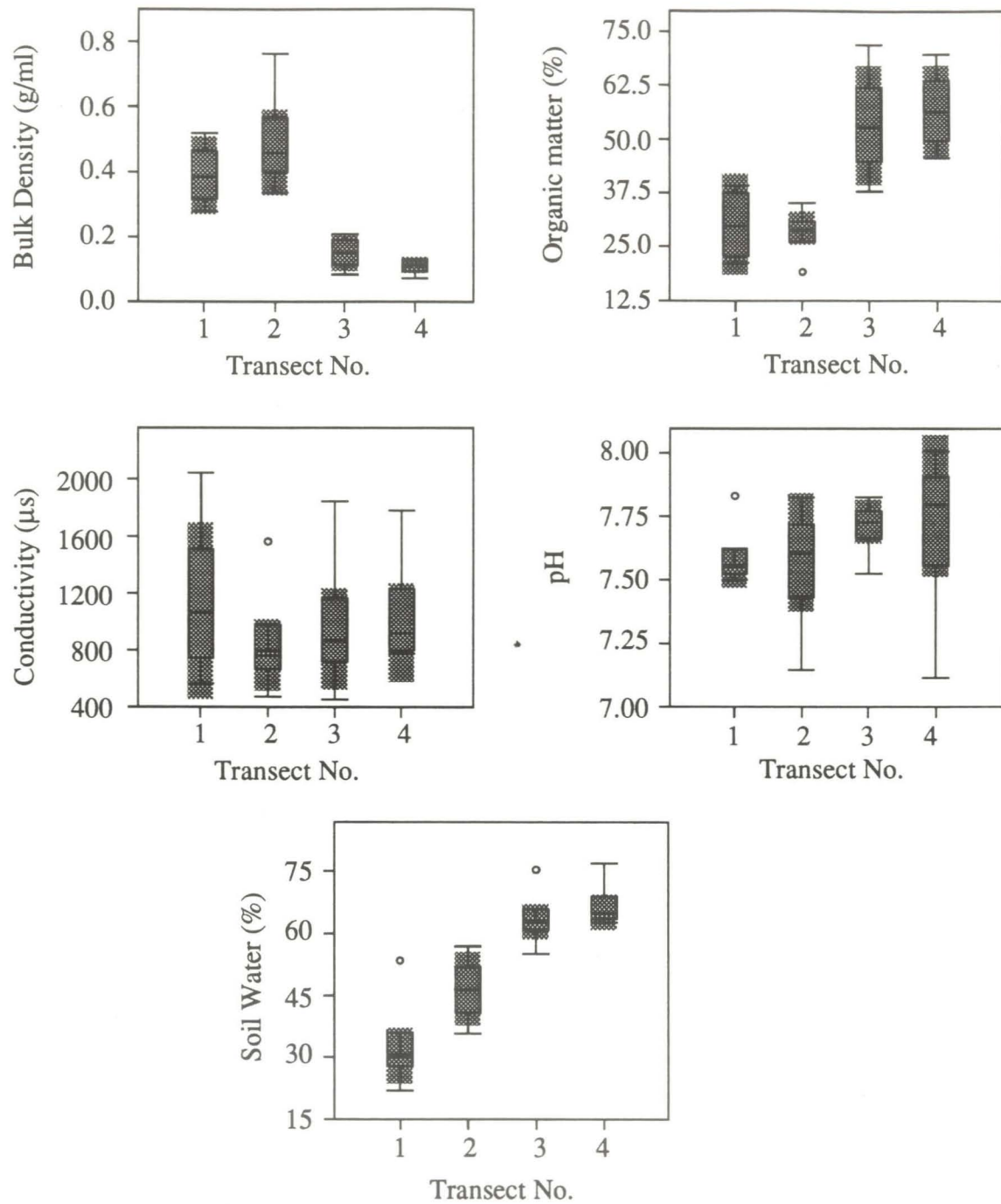


Figure A 1.15 Boxplots of within-meadow variation in soil factors, meadow 15.

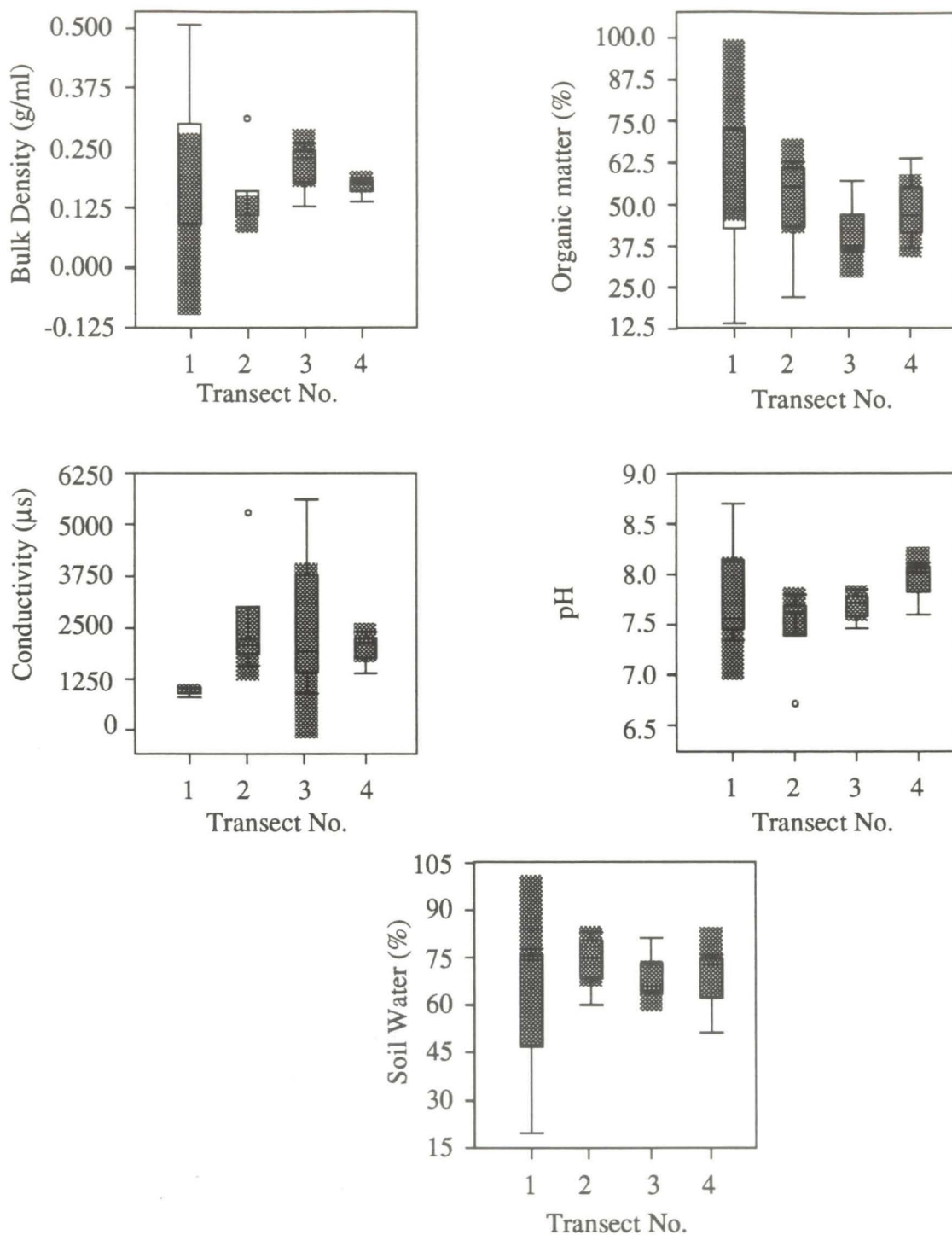


Figure A 1.11 Boxplots of within-meadow variation in soil factors, meadow p4.

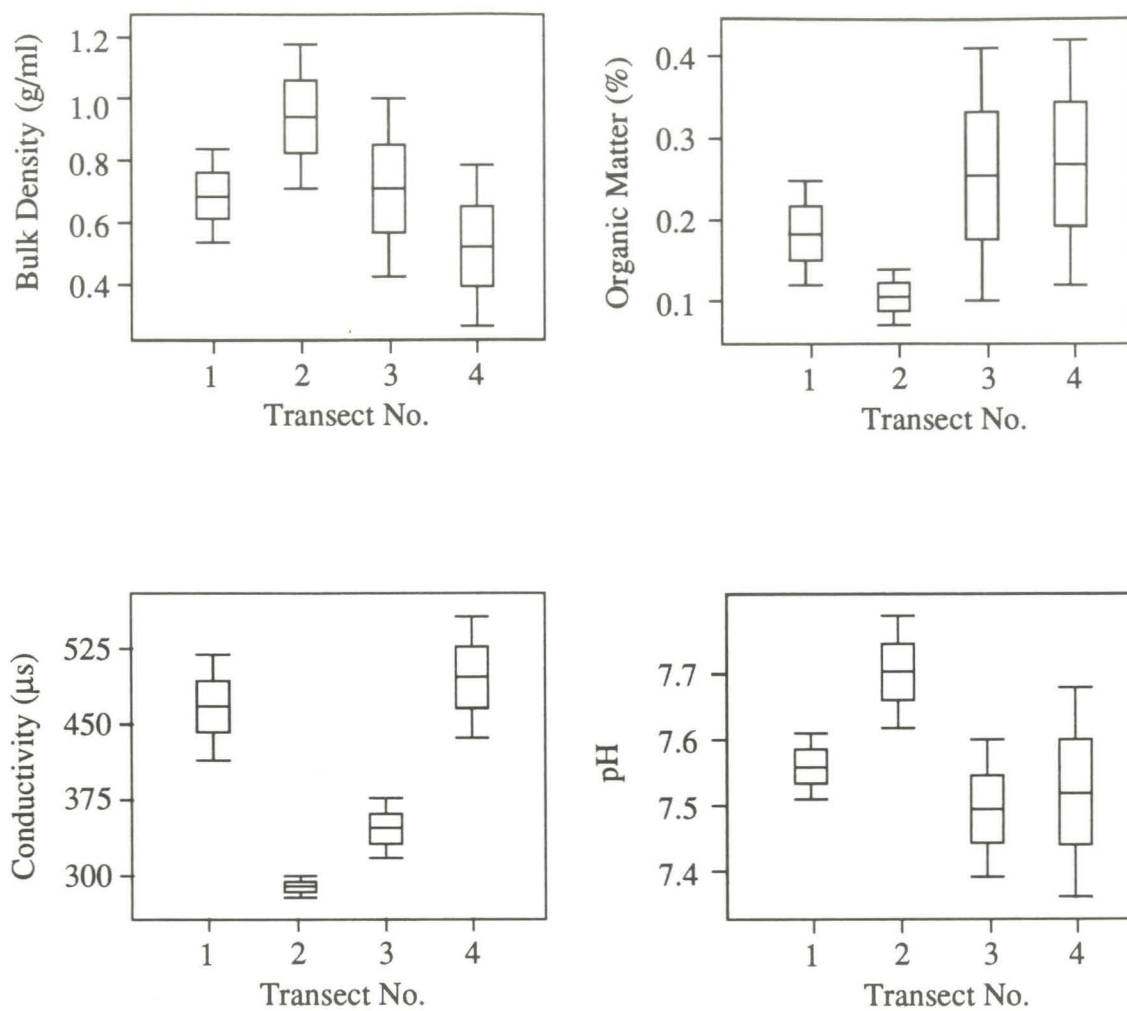


Figure A 1.12 Boxplots of within-pond variation in soil factors, pond 1.

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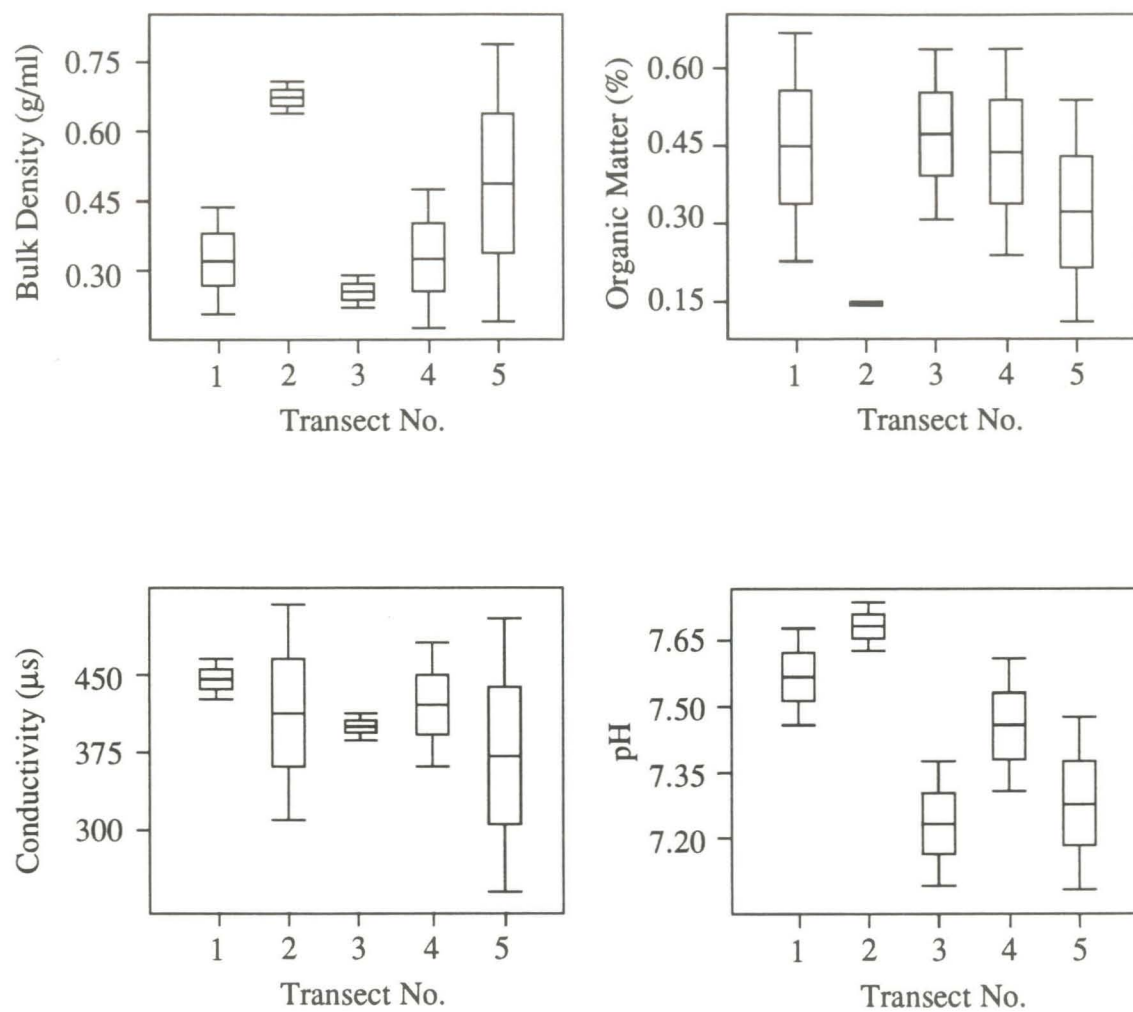


Figure A 1.13 Boxplots of within-pond variation in soil factors, pond 2.

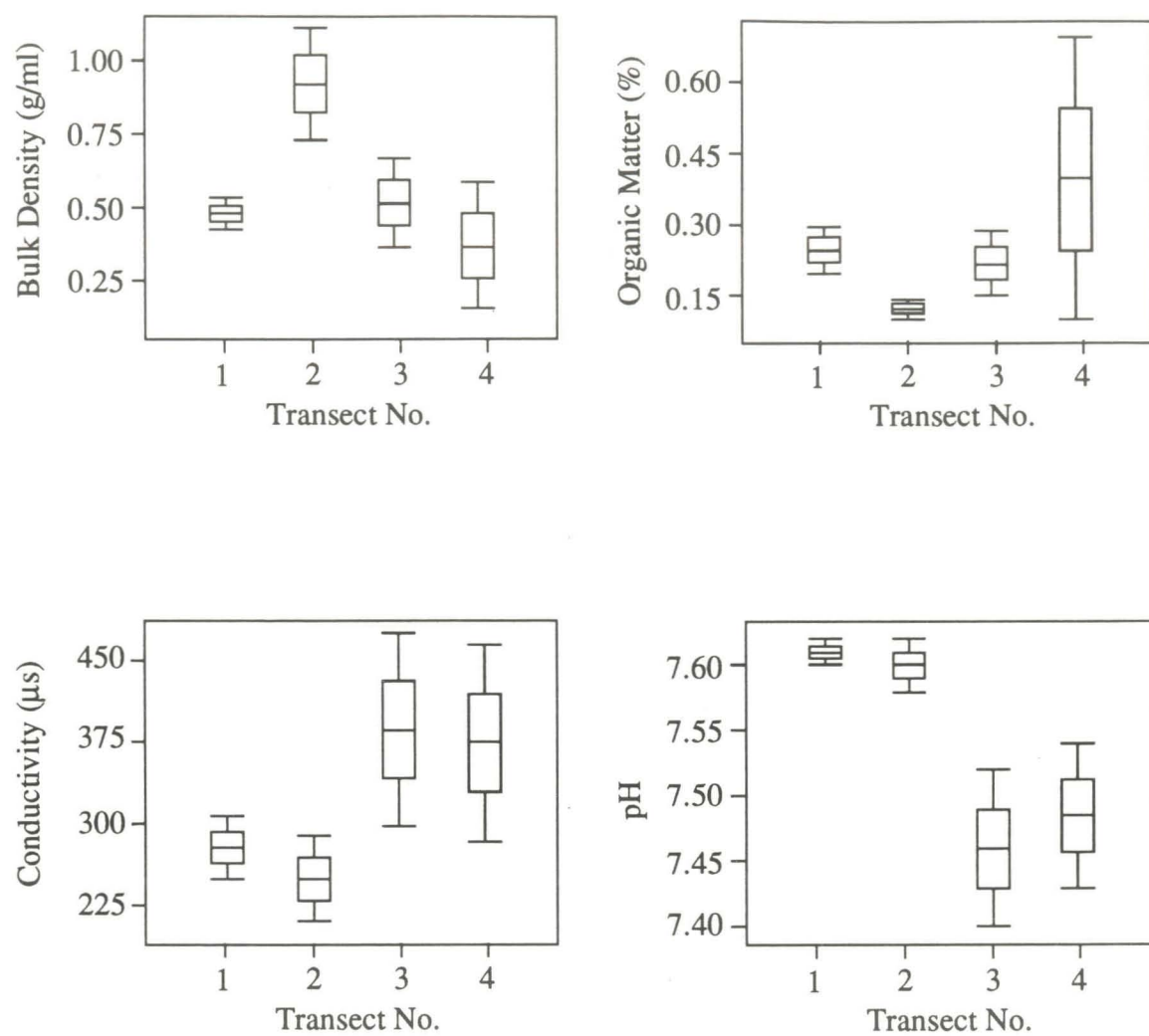


Figure A 1.14 Boxplots of within-pond variation in soil factors, pond 3.

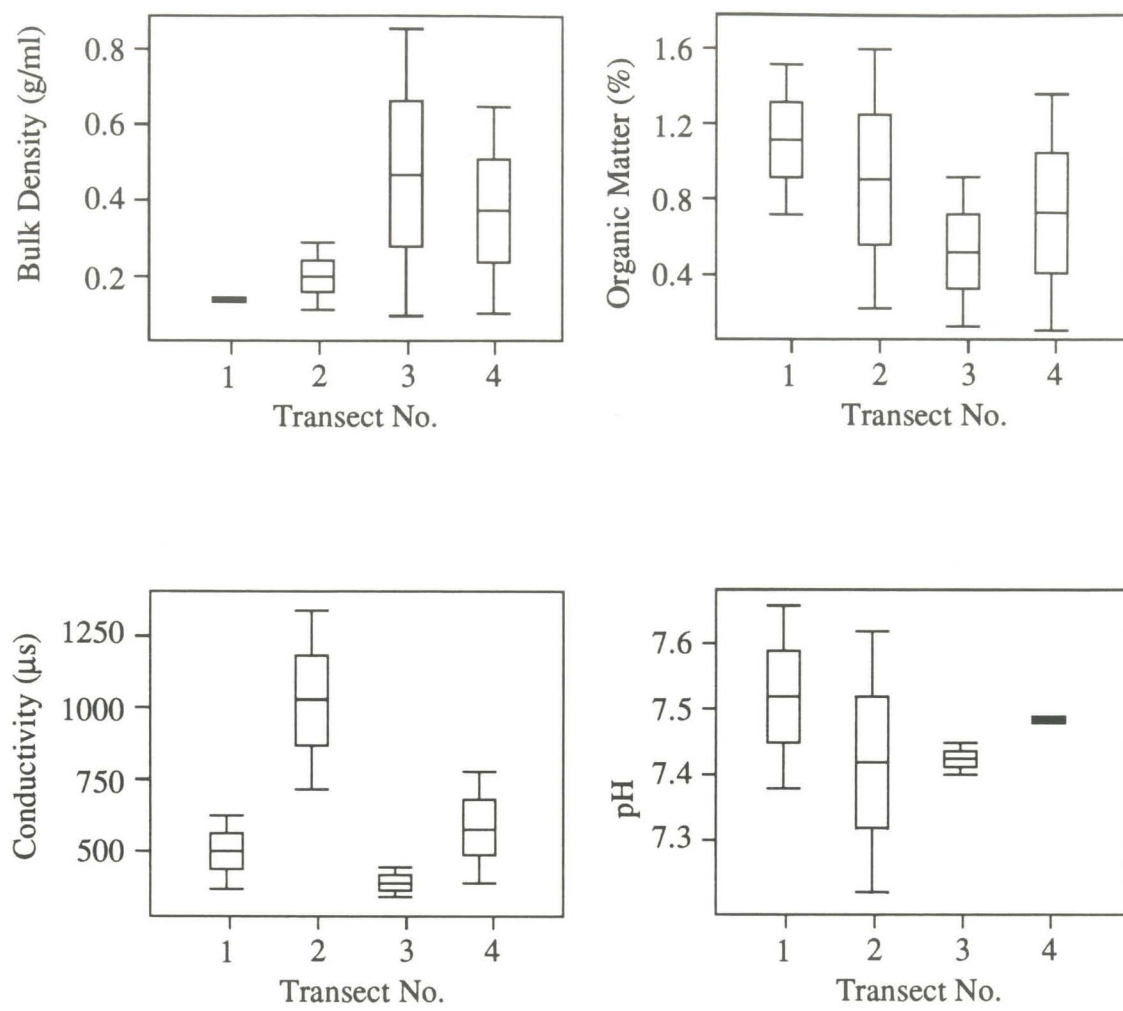


Figure A 1.15 Boxplots of within-pond variation in soil factors, pond 4.

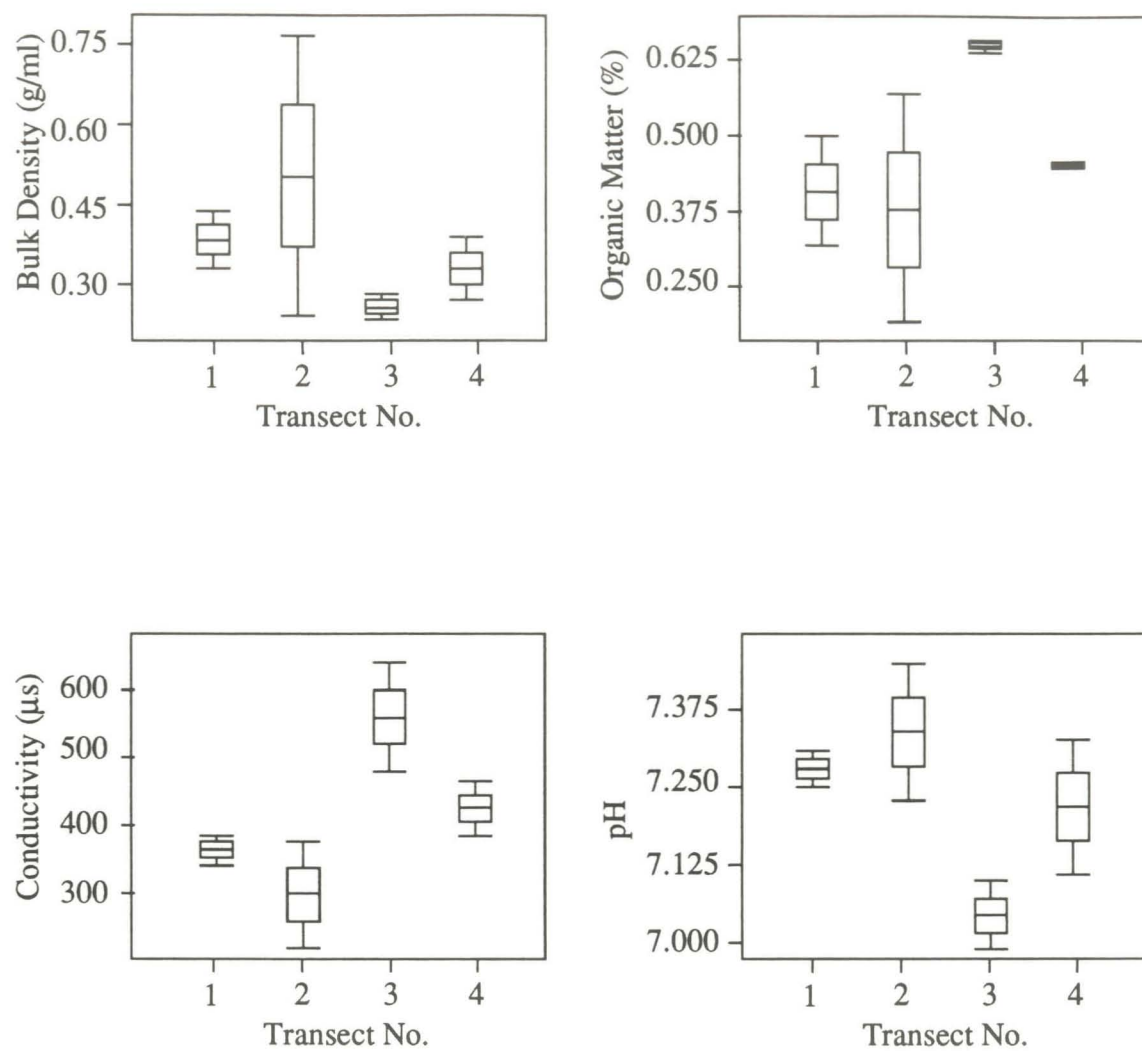


Figure A 1.16 Boxplots of within-pond variation in soil factors, pond 6.

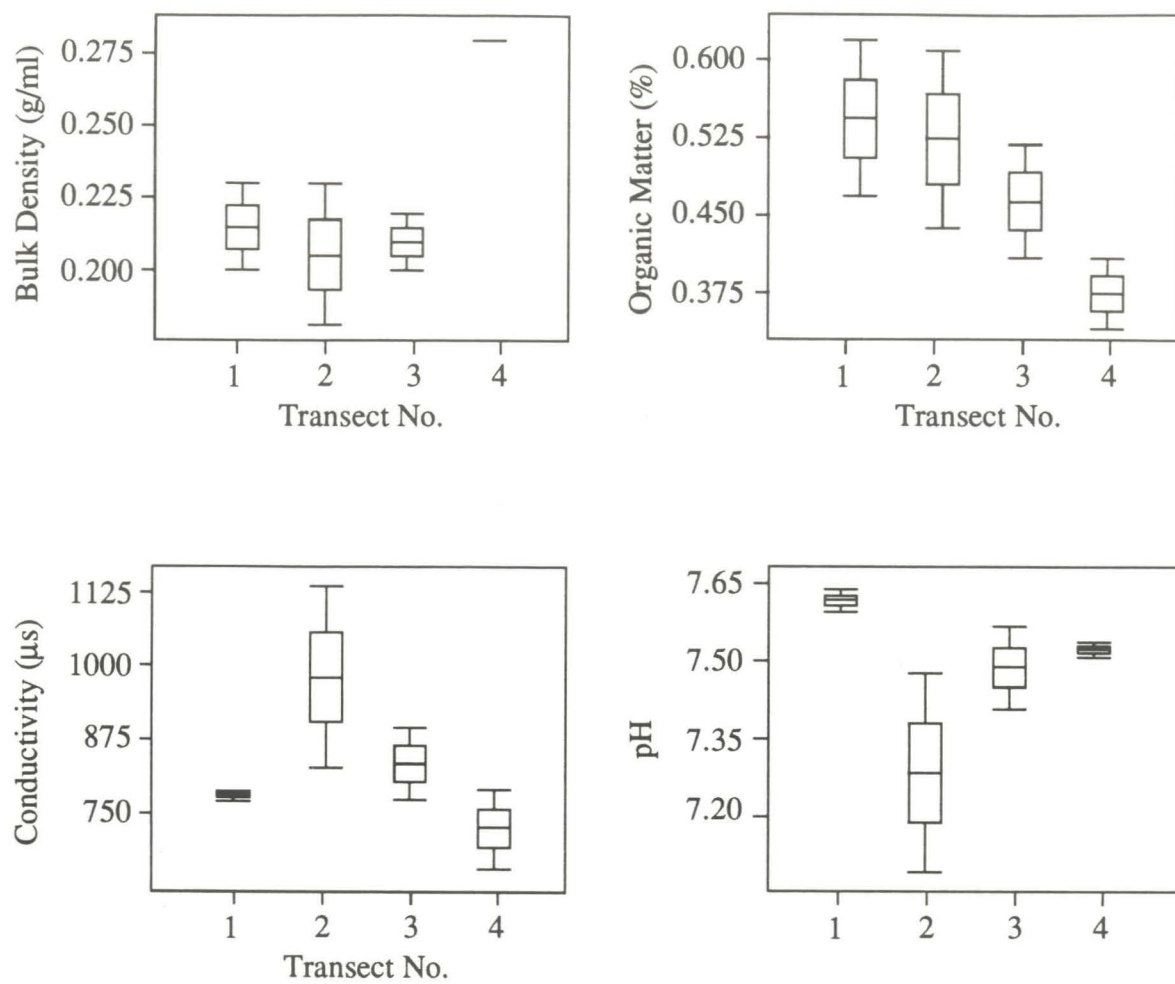


Figure A 1.17 Boxplots of within-pond variation in soil factors, pond 7.

Appendix 2.1 Soil chemistry data for full ponds						
Pond	Transect	Sample	Organic Matter (%)	Bulk Density (g/ml)	Conductivity (μ s)	pH
1	1	7	24.88	0.54	416	7.61
1	1	2	12.42	0.84	521	7.51
1	2	2	7.50	1.18	299	7.62
1	2	6	14.39	0.71	278	7.79
1	3	6	9.60	1.00	377	7.60
1	3	1	41.05	0.43	319	7.39
1	4	5	41.83	0.26	557	7.36
1	4	1	12.01	0.79	438	7.68
2	1	6	22.89	0.44	428	7.68
2	1	1	66.56	0.21	467	7.46
2	2	6	15.49	0.64	519	7.63
2	2	1	14.46	0.71	311	7.74
2	3	1	64.33	0.22	388	7.09
2	3	7	30.97	0.29	414	7.38
2	4	6	23.67	0.48	363	7.61
2	4	1	63.91	0.18	481	7.31
2	5	6	11.09	0.79	240	7.48
2	5	1	53.95	0.19	505	7.08
3	1	6	19.61	0.43	309	7.62
3	1	1	30.14	0.54	249	7.60
3	2	1	10.42	1.12	209	7.58
3	2	6	13.83	0.73	290	7.62
3	3	1	14.94	0.67	299	7.52
3	3	6	28.63	0.37	476	7.40
3	4	1	69.82	0.15	465	7.54
3	4	6	10.49	0.59	285	7.43
4	1	6	35.59	0.28	629	7.66
4	1	1	75.66	0.26	365	7.38
4	2	1	80.28	0.22	1342	7.22
4	2	6	11.36	0.58	717	7.62
4	3	5	5.96	1.71	334	7.40
4	3	1	46.32	0.18	442	7.45
4	4	1	67.63	0.20	780	7.48
4	4	5	4.63	1.30	386	7.49
6	1	5	49.91	0.33	388	7.31
6	1	1	31.57	0.44	343	7.25
6	2	5	57.28	0.24	378	7.23
6	2	1	18.51	0.77	219	7.45
6	3	1	64.03	0.28	481	7.10
6	3	4	66.25	0.23	642	6.99
6	4	6	46.20	0.27	465	7.11
6	4	1	45.05	0.39	388	7.33
7	1	1	62.40	0.23	773	7.60
7	1	6	46.50	0.20	790	7.64
7	2	7	43.62	0.23	828	7.48
7	2	1	60.76	0.18	1138	7.09
7	3	9	51.83	0.22	776	7.57
7	3	1	41.05	0.20	896	7.41
7	4	1	34.19	0.28	792	7.54
7	4	3	41.31	0.28	655	7.51

Appendix 2.2 Soil chemistry data for meadows							
Meadow	Transect	Sample	Soil Water (%)	Bulk Density (g/ml)	Conductivity (μ s)	pH	Organic Matter (%)
1	1	1	27.43	0.43	1489	7.20	22.98
1	1	4	46.10	0.47	1208	7.98	21.01
1	1	6	23.60	0.26	557	7.36	27.81
1	1	9	55.65	0.55	614	8.33	25.58
1	2	3	34.90	0.73	275	7.94	
1	2	4	63.14	0.42	653	7.83	22.16
1	2	6	47.16	0.40	496	7.67	17.52
1	2	9	27.83	0.71	260	7.88	24.07
1	3	1	59.89	0.29	1053	7.82	56.22
1	3	4	46.18	0.43	885	8.08	31.86
1	3	6	53.06	0.43	1517	7.81	38.92
1	3	10	50.47	0.32	660	7.86	27.52
1	4	1	75.24	0.11	954	7.61	57.14
1	4	3	72.15	0.13	1502	8.25	66.03
1	4	5	71.86	0.24	544	7.21	36.43
1	4	7	60.81	0.40	829	7.50	32.74
1	5	1	60.66	0.18	1308	8.08	59.94
1	5	3	52.79	0.27	895	7.75	29.26
1	5	5	67.95	0.22	2080	7.63	44.89
2	1	1	28.00	0.39	1505	7.66	29.43
2	1	4	61.71	0.16	1526	8.29	47.43
2	1	7	37.96	0.32	850	7.96	29.29
2	2	1	38.60	0.54	398	7.89	20.37
2	2	4	48.95	0.40	594	8.06	30.97
2	2	7	48.47	0.42	537	7.93	26.02
2	3	1	65.74	0.17	1234	7.83	55.06
2	3	4	69.07	0.33	1778	7.75	35.35
2	3	6	63.39	0.32	906	7.85	27
2	3	9	71.79	0.17	1050	7.98	45.67
2	4	1	71.75	0.14	720	8.30	54.75
2	4	3	72.77	0.23	1188	7.71	42.6
2	4	6	72.49	0.22	725	7.60	39.13
2	4	8	74.68	0.16	1093	8.56	54.57
2	5	1	69.05	0.13	1121	8.01	54.73
2	5	4	59.39	0.29	923	7.98	21.54
2	5	6	46.87	0.36	2360	7.88	44.55
2	5	8	61.07	0.25	837	8.02	45.21
3	1	1	55.76	0.27	988	7.78	39.71
3	1	4	49.39	0.29	2560	7.17	
3	1	6	47.08	0.50	800	7.73	28.87
3	2	1	75.97	0.17	1011	8.37	49.39
3	2	4	57.12	0.46	647	7.89	25.22
3	2	6	59.49	0.20	689	8.48	32.69
3	3	1	73.20	0.26	1377	7.96	48.09
3	3	3	65.80	0.19	1214	7.84	40.03
3	4	1	41.99	0.49	685	7.93	36.49
3	4	3	65.38	0.19	1185	7.98	49.3
5	1	1	28.66	0.23	665	7.97	39.3
5	1	5	37.15	0.33	921	7.96	42.82
5	1	7	50.06	0.49	536	7.90	28.08
5	2	1	34.65	1.00	398	7.67	11.26
5	2	3	65.02	0.26	817	7.89	32.24

Appendix 2.2 Soil chemistry data for meadows							
Meadow	Transect	Sample	Soil Water (%)	Bulk Density (g/ml)	Conductivity (µs)	pH	Organic Matter (%)
5	2	5	73.11	0.27	901	7.23	46.31
5	2	7	71.19	0.28	816	7.63	45.99
5	3	3	45.35	0.58	489	8.29	14.8
5	3	5	75.47	0.19	1040	8.70	50.57
5	4	1	61.83	0.17	805	7.72	53.8
5	4	3	50.10	0.49	595	7.83	12.78
5	4	5	78.82	0.18	1169	7.95	47.89
7	1	1	55.03	0.50	609	8.46	25.3
7	1	3	46.49	0.29	481	7.59	23.81
7	1	5	63.15	0.40	609	8.07	30.38
7	2	1	58.36	0.44	1583	7.16	23.09
7	2	3	70.95	0.26	2240	7.23	33.54
7	2	5	73.84	0.16	1024	7.38	53.68
7	2	7	82.18	0.13	794	8.52	63.37
7	3	1	64.64	0.13	1144	7.95	48.21
7	3	3	67.28	0.18	1008	7.99	47.53
7	3	5	74.48	0.12	1313	8.01	54.87
7	4	1	80.54	0.14	616	7.77	20.18
7	4	3	35.24	0.36	404	7.64	20.91
7	4	6	81.66	0.14	1199	8.49	68.73
8	1	1	59.22	0.28	982	7.83	16.66
8	1	4	58.16	0.43	533	7.75	30.92
8	1	6	55.90	0.23	745	7.79	40.95
8	1	13	69.40	0.36	1205	8.18	30.37
8	2	3	45.32	0.67	781	8.29	16.49
8	2	7	56.66	0.39	648	7.42	27.77
8	2	10	65.04	0.34	1005	8.07	32.52
8	2	12	64.26	0.30	1208	7.26	31.35
8	3	2	73.75	0.17	770	7.81	61.12
8	3	5	65.20	0.17	898	7.93	35.41
8	3	7	54.83	0.23	749	7.82	29.49
8	3	9	59.13	0.36	648	7.89	59.84
8	4	1	75.54	0.11	985	7.55	58.65
8	4	4	67.20	0.15	249	8.43	47.4
8	4	7	69.87	0.16	941	8.31	42.46
8	5	1	45.93	0.48	532	8.19	21.59
8	5	5	59.28	0.40	562	7.13	39.65
8	5	7	72.17	0.20	1280	8.57	45.35
11	1	1	27.57	0.57	299	7.57	10.38
11	1	3	39.41	0.42	604	7.53	20.32
11	1	5	38.20	0.37	1188	7.64	20.13
11	1	7	39.25	0.31	675	8.31	26.63
11	2	1	50.62	0.18	546	7.39	28.36
11	2	3	39.97	0.37	819	7.60	12.53
11	2	5	59.20	0.15	1248	7.80	35.19
11	2	7	40.34	0.33	683	7.41	25.52
11	2	2a	63.39	0.26	1630	7.58	25.81
11	2	2c	48.28	0.37	744	7.71	16.23
11	3	1	48.60	0.32	581	7.45	31.4
11	3	3	53.70	0.33	477	7.71	28.05
11	3	5	69.09	0.22	1203	7.83	57.49
11	3	7	71.18	0.20	748	7.65	61.62

Appendix 2.2 Soil chemistry data for meadows							
Meadow	Transect	Sample	Soil Water (%)	Bulk Density (g/ml)	Conductivity (μ S)	pH	Organic Matter (%)
11	4	1	69.27	0.19	729	7.75	5.4
11	4	3	47.51	0.47	435	7.77	19.25
11	4	4	37.62	0.50	589	7.70	
11	4	6	70.36	0.15	872	7.72	54.42
12	1	1	48.36	0.23	1068	7.90	44.38
12	1	3	60.58	0.15	951	8.02	51.67
12	1	6	45.94	0.21	1228	8.08	48.2
12	1	8	44.67	0.28	1152	7.84	25.82
12	2	1	58.69	0.25	641	7.68	32.53
12	2	3	61.16	0.21	951	7.48	37.69
12	2	6	61.14	0.26	1530	7.66	26.12
12	2	8	52.90	0.39	1471	7.63	18.96
12	3	1	78.88	0.14	964	7.88	64.94
12	3	3	77.94	0.19	1203	7.86	53.19
12	4	1	79.70	0.13	1217	7.93	58.5
12	4	3	77.51	0.14	806	7.92	47.11
12	4	5	71.04	0.17	1192	7.64	40.28
14	1	1	74.09	0.12	1013	8.66	72.34
14	1	4	49.19	0.33	1912	8.19	25.67
14	1	6	50.20	0.18	1134	7.75	36.34
14	2	1	28.53	0.64	195	7.90	8.82
14	2	4	65.30	0.30	755	7.82	22.48
14	2	6	57.66	0.36	690	7.81	17.26
14	3	1	81.92	0.13	1302	7.54	68.44
14	3	3	72.92	0.14	1155	7.53	42.97
14	3	5	73.22	0.18	1290	7.64	42.56
14	4	2	68.98	0.31	757	7.36	30.97
14	4	4	66.70	0.38	603	8.34	31.62
14	4	6	67.00	0.29	784	7.29	35.39
15	1	1	21.75	0.52	556	7.54	21.23
15	1	3	53.37	0.45	1346	7.56	23.15
15	1	6	29.52	0.28	796	7.50	37.02
15	1	9	30.89	0.33	2050	7.83	39.68
15	2	1	35.86	0.50	723	7.53	19.1
15	2	3	42.75	0.77	471	7.83	35.54
15	2	6	57.15	0.42	1568	7.69	28.87
15	2	9	50.58	0.34	790	7.14	29.81
15	3	1	55.36	0.18	449	7.53	38.22
15	3	4	63.08	0.12	948	7.75	47.32
15	3	7	62.65	0.21	1851	7.71	59.16
15	3	9	75.31	0.08	807	7.83	72.36
15	4	1	66.51	0.10	771	7.11	61.51
15	4	4	62.95	0.12	799	7.71	45.77
15	4	7	63.88	0.13	1053	7.88	51.33
15	4	9	77.05	0.07	1785	8.01	70.21
p4	1	1	77.77	0.09	810	8.72	72.24
p4	1	4	19.28	0.51	996	7.36	14.05
p4	1	7	74.28	0.09	1044	7.56	73.22
p4	2	1	83.04	0.11	2240	7.65	60.54
p4	2	4	60.36	0.31	1954	7.62	21.84
p4	2	7	79.52	0.11	5310	6.71	63.04
p4	2	2b	71.15	0.11	1613	7.80	50.66

Appendix 2.2 Soil chemistry data for meadows							
Meadow	Transect	Sample	Soil Water (%)	Bulk Density (g/ml)	Conductivity (μ S)	pH	Organic Matter (%)
p4	3	1	63.60	0.23	910	7.85	37.64
p4	3	2	65.97	0.26	5640	7.46	36.04
p4	3	5	81.25	0.13	1928	7.71	57.11
p4	4	1	73.14	0.14	2140	8.04	64.06
p4	4	2	51.32	0.19	1412	7.61	37.36
p4	4	4	76.03	0.18	2430	8.12	46.7

Appendix 2.3 Frequency of seeds found in the full pond seed bank

Pond No.	1	1	1	1	2	2	2
Transect No.	1	2	3	4	1	2	3
Species							
<i>Alnus rugosa</i>	0	0	0	0	0.167	0	0
<i>Anemone canadensis</i>	0	0	0	0	0	0	0
<i>Aster junciformis</i>	0	0	0.125	0.286	0.083	0.083	0.1
<i>Beckmannia syzigachne</i>	0	0	0	0	0	0	0
<i>Bidens cernua</i>	0.4	0.125	0	0.143	0	0	0
<i>Calamagrostis canadensis</i>	0	0	0	0	0	0	0
<i>Carex aquatilis</i>	0	0.25	0.25	0.286	0.083	0.167	0
<i>Carex atherodes</i>	0.2	0	0.25	0.286	0	0.417	0.1
<i>Carex rostrata</i>	0	0	0	0.143	0.083	0	0.1
<i>Carex sespitosis</i>	0.1	0	0	0	0	0.083	0
<i>Chenopodium rubrum</i>	0.4	0.25	0.125	0.571	0.083	0	0
<i>Cirsium arvense</i>	0	0	0	0	0.083	0	0.1
<i>Epilobium glandulosum</i>	0	0	0	0	0.083	0	0
<i>Fragaria hairy</i>	0	0	0	0	0	0	0
<i>Fragaria smooth</i>	0	0	0	0	0.083	0	0
<i>Galeopsis tetrahit</i>	0	0	0	0	0	0	0
<i>Galium trifidum</i>	0.6	0.5	0.125	0.429	0.167	0	0
<i>Geum aleppicum</i>	0	0	0	0	0	0	0
<i>Lycopus uniflorus</i>	0	0	0	0	0	0	0
<i>Medicago lupulina</i>	0	0	0	0	0.167	0.083	0
<i>Mentha arvensis</i>	0.2	0	0	0	0.083	0	0
<i>Mimulus ringers</i>	0.2	0	0	0	0	0	0
<i>Picae glauca</i>	0	0	0	0	0	0	0
<i>Plantago major</i>	0	0	0	0	0.25	0	0
<i>Poa palustris</i>	0.5	0.375	0.25	0.143	0.833	0.333	0.1
<i>Polygonum lapathifolium</i>	0.2	0.125	0	0	0	0	0
<i>Potentilla norvegica</i>	0	0	0	0	0	0	0
<i>Ranunculus aquatilis</i>	0.1	0	0	0	0	0	0
<i>Ranunculus sceleratus</i>	0	0.375	0	0.429	0.167	0	0
<i>Rorippa islandica</i>	0.2	0.125	0	0.143	0.167	0	0
<i>Rubus strigosus</i>	0	0	0	0	0	0	0
<i>Rumex maritimus</i>	0.4	0.125	0.125	0	0	0	0
<i>Rumex occidentalis</i>	0.1	0	0	0	0	0	0
<i>Sagittaria cuneata</i>	0	0	0	0	0	0.083	0
<i>Salix gracilis</i>	0	0	0	0	0	0	0
<i>Sium suave</i>	0.1	0	0	0.143	0	0	0
<i>Solidago canadensis</i>	0	0	0	0	0.083	0	0
<i>Sonchus arvensis</i>	0	0.125	0	0	0.667	0	0.1
<i>Stachys palustris</i>	0.1	0	0	0	0	0	0
<i>Taraxacum officinale</i>	0	0	0	0	0.083	0	0
<i>Trifolium repens</i>	0	0	0	0	0.083	0	0
<i>Typha latifolia</i>	0	0	0	0	0	0	0
<i>Urtica dioica</i>	0.4	0.125	0.125	0.286	0.167	0	0
<i>Vicia americana</i>	0	0	0	0	0	0	0

Appendix 2.3

Pond No.	2	2	3	3	3	3	4
Transect No.	4	5	1	2	3	4	1
Species							
<i>Alnus rugosa</i>	0	0	0	0.1	0.1	0.091	0
<i>Anemone canadensis</i>	0	0	0	0	0	0	0
<i>Aster junciformis</i>	0	0	0	0	0.2	0	0
<i>Beckmannia syzigachne</i>	0	0	0.091	0	0	0.091	0
<i>Bidens cernua</i>	0	0	0.182	0.1	0.1	0.091	0
<i>Calamagrostis canadensis</i>	0	0	0	0	0	0	0.125
<i>Carex aquatilis</i>	0.364	0.436	0.273	0.2	0.3	0.091	0
<i>Carex atherodes</i>	0	0.1	0	0.1	0.1	0.091	0
<i>Carex rostrata</i>	0.182	0.218	0.091	0	0	0.091	0
<i>Carex sespitosis</i>	0.091	0.009	0	0	0	0	0
<i>Chenopodium rubrum</i>	0	0	0.364	0.2	0.1	0.455	0
<i>Cirsium arvense</i>	0	0.1	0	0	0	0.091	0
<i>Epilobium glandulosum</i>	0	0	0.091	0.1	0.1	0	0
<i>Fragaria hairy</i>	0.091	0.009	0.091	0.1	0.1	0.182	0
<i>Fragaria smooth</i>	0	0	0.364	0.1	0.1	0.364	0.125
<i>Galeopsis tetrahit</i>	0	0	0	0	0	0	0.125
<i>Galium trifidum</i>	0	0	0.636	0.2	0.4	0.455	0
<i>Geum aleppicum</i>	0	0	0	0	0	0	0
<i>Lycopus uniflorus</i>	0	0	0	0.1	0	0	0
<i>Medicago lupulina</i>	0	0	0	0	0	0	0
<i>Mentha arvensis</i>	0	0	0.364	0	0	0.273	0.125
<i>Mimulus ringers</i>	0	0	0	0	0.1	0.273	0
<i>Picae glauca</i>	0	0	0	0	0	0	0
<i>Plantago major</i>	0	0	0	0.1	0	0	0
<i>Poa palustris</i>	0	0.3	0.636	0.7	0.5	0.818	0.375
<i>Polygonum lapathifolium</i>	0.091	0.009	0	0	0	0	0
<i>Potentilla norvegica</i>	0	0	0	0	0.1	0	0
<i>Ranunculus aquatilis</i>	0	0	0	0	0	0	0
<i>Ranunculus sceleratus</i>	0	0.1	0	0.1	0.1	0.091	0.125
<i>Rorippa islandica</i>	0	0.2	0	0	0.1	0.091	0
<i>Rubus strigosus</i>	0	0	0	0	0	0	0
<i>Rumex maritimus</i>	0	0	0.091	0	0	0.182	0
<i>Rumex occidentalis</i>	0	0	0	0	0	0	0
<i>Sagittaria cuneata</i>	0	0	0	0	0	0	0
<i>Salix gracilis</i>	0	0	0	0	0	0	0
<i>Sium suave</i>	0	0	0.091	0	0	0	0
<i>Solidago canadensis</i>	0	0	0	0	0	0	0.125
<i>Sonchus arvensis</i>	0	0	0.091	0	0	0	0
<i>Stachys palustris</i>	0	0	0	0	0	0	0.125
<i>Taraxacum officinale</i>	0	0	0	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0	0	0	0
<i>Typha latifolia</i>	0.091	0.009	0	0	0	0	0
<i>Urtica dioica</i>	0.182	0.018	0.545	0.1	0	0.273	0.375
<i>Vicia americana</i>	0	0	0	0	0	0	0

Appendix 2.3

Pond No.	4	4	4	6	6	6	6
Transect No.	2	3	4	1	2	3	4
Species							
<i>Alnus rugosa</i>	0	0	0	0	0.091	0.111	0
<i>Anemone canadensis</i>	0	0	0	0.091	0	0.111	0
<i>Aster junciformis</i>	0	0	0.125	0	0	0	0.111
<i>Beckmannia syzigachne</i>	0	0	0	0	0.091	0	0.111
<i>Bidens cernua</i>	0	0.143	0	0	0	0	0
<i>Calamagrostis canadensis</i>	0.018	0.286	0	0	0	0	0
<i>Carex aquatilis</i>	0.143	0.143	0	0.182	0.455	0.333	0.444
<i>Carex atherodes</i>	0	0	0	0	0	0.333	0
<i>Carex rostrata</i>	0	0	0	0	0	0	0
<i>Carex sespitosis</i>	0	0	0	0.091	0	0	0
<i>Chenopodium rubrum</i>	0	0.143	0.125	0.091	0.182	0	0
<i>Cirsium arvense</i>	0	0	0.125	0.091	0	0	0
<i>Epilobium glandulosum</i>	0.143	0	0	0	0	0	0
<i>Fragaria hairy</i>	0.143	0.143	0	0.091	0	0	0.333
<i>Fragaria smooth</i>	0.161	0	0.125	0.273	0.455	0.333	0.333
<i>Galeopsis tetrahit</i>	0.018	0	0.125	0.182	0	0	0
<i>Galium trifidum</i>	0	0.286	0	0.273	0.273	0.333	0.444
<i>Geum aleppicum</i>	0	0	0	0.091	0	0	0
<i>Lycopus uniflorus</i>	0.143	0	0	0.091	0	0	0
<i>Medicago lupulina</i>	0	0	0	0	0	0	0
<i>Mentha arvensis</i>	0.446	0.429	0.25	0.455	0.182	0.222	0.111
<i>Mimulus ringers</i>	0.143	0	0.125	0.182	0.182	0	0.222
<i>Picea glauca</i>	0	0	0	0	0	0	0.111
<i>Plantago major</i>	0	0	0	0	0	0.111	0
<i>Poa palustris</i>	0.482	0.286	0.5	0.727	0.182	0.333	0.333
<i>Polygonum lapathifolium</i>	0	0	0	0	0	0	0
<i>Potentilla norvegica</i>	0	0	0	0.182	0.091	0.333	0
<i>Ranunculus aquatilis</i>	0	0	0	0	0	0	0
<i>Ranunculus sceleratus</i>	0.304	0.143	0	0.182	0.182	0.333	0.333
<i>Rorippa islandica</i>	0	0.143	0	0.727	0.273	0.556	0.222
<i>Rubus strigosus</i>	0	0	0	0	0	0.111	0
<i>Rumex maritimus</i>	0.143	0	0	0.273	0.273	0.222	0.222
<i>Rumex occidentalis</i>	0	0	0	0	0	0	0
<i>Sagittaria cuneata</i>	0	0	0	0	0	0	0
<i>Salix gracilis</i>	0	0	0	0	0.091	0	0
<i>Sium suave</i>	0.143	0.143	0	0.091	0.091	0.111	0
<i>Solidago canadensis</i>	0.018	0	0	0	0	0.111	0
<i>Sonchus arvensis</i>	0	0	0.125	0	0	0	0
<i>Stachys palustris</i>	0.161	0	0.125	0	0	0	0.111
<i>Taraxacum officinale</i>	0	0.143	0	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0	0	0	0
<i>Typha latifolia</i>	0	0	0	0	0	0	0
<i>Urtica dioica</i>	0.768	0.571	0.75	0.545	0.091	0.222	0.111
<i>Vicia americana</i>	0	0	0	0.091	0	0	0

Appendix 2.3

Pond No.	7	7	7	7
Transect No.	1	2	3	4
Species				
<i>Alnus rugosa</i>	0	0	0.071	0
<i>Anemone canadensis</i>	0	0	0	0
<i>Aster junciformis</i>	0	0	0	0
<i>Beckmannia syzigachne</i>	0	0	0	0
<i>Bidens cernua</i>	0.25	0.071	0	0
<i>Calamagrostis canadensis</i>	0	0	0	0
<i>Carex aquatilis</i>	0.313	0.214	0.214	0.222
<i>Carex atherodes</i>	0.25	0.214	0.143	0.333
<i>Carex rostrata</i>	0.063	0.071	0.071	0
<i>Carex sespitosis</i>	0.063	0	0	0
<i>Chenopodium rubrum</i>	0.063	0	0	0
<i>Cirsium arvense</i>	0	0.214	0	0
<i>Epilobium glandulosum</i>	0.063	0	0	0
<i>Fragaria hairy</i>	0.063	0	0	0
<i>Fragaria smooth</i>	0.063	0	0	0.111
<i>Galeopsis tetrahit</i>	0	0	0	0
<i>Galium trifidum</i>	0.438	0	0.071	0.111
<i>Geum aleppicum</i>	0	0	0	0
<i>Lycopus uniflorus</i>	0.188	0	0	0
<i>Medicago lupulina</i>	0	0	0	0
<i>Mentha arvensis</i>	0.375	0.071	0.143	0.222
<i>Mimulus ringers</i>	0.063	0	0	0.111
<i>Picea glauca</i>	0	0	0	0
<i>Plantago major</i>	0	0	0	0
<i>Poa palustris</i>	0.438	0.286	0.143	0.111
<i>Polygonum lapathifolium</i>	0.063	0	0	0
<i>Potentilla norvegica</i>	0	0	0	0
<i>Ranunculus aquatilis</i>	0	0	0	0
<i>Ranunculus sceleratus</i>	0.125	0	0	0.111
<i>Rorippa islandica</i>	0.125	0.286	0	0
<i>Rubus strigosus</i>	0	0	0	0
<i>Rumex maritimus</i>	0.375	0.357	0.071	0.333
<i>Rumex occidentalis</i>	0	0	0.071	0
<i>Sagittaria cuneata</i>	0	0.214	0	0.111
<i>Salix gracilis</i>	0	0	0	0
<i>Sium suave</i>	0	0.071	0	0
<i>Solidago canadensis</i>	0	0	0	0
<i>Sonchus arvensis</i>	0	0	0	0
<i>Stachys palustris</i>	0.063	0	0	0
<i>Taraxacum officinale</i>	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0
<i>Typha latifolia</i>	0.063	0	0	0
<i>Urtica dioica</i>	0.625	0.071	0.143	0.111
<i>Vicia americana</i>	0	0	0	0

Appendix 2.4 Species seed frequencies in the cold treated meadow samples

Meadow	1	1	1	1	1	2	2	2
Transect	1	2	3	4	5	1	2	3
Species								
<i>Agrostis scabra</i>	0	0	0	0	0	0	0	0
<i>Alopecurus aequalis</i>	0.25	0	0	0	0.333	0	0	0
<i>Amaranthus retroflexus</i>	0.25	0.75	0.333	0.2	0.667	0.333	0.667	0.5
<i>Aster simplex</i>	0	0	0	0.2	0	0	0	0
<i>Bidens cernua</i>	0.25	0	0	0	0	0	0	0
<i>Beckmannia syzigachne</i>	0	0	0	0	0.333	0	0	0
<i>Bromus inermis</i>	0	0	0	0	0	0	0	0
<i>Carex atherodes</i>	0	0.25	0	0	0	0	0.667	0
<i>Carex aquatilis</i>	0.25	0	0	0	0	0.333	0	0
<i>Carex sychnocephala</i>	0	0	0	0	0	0	0	0
<i>Carex rostrata</i>	0	0	0	0	0.333	0	0	0
<i>Chenopodium rubrum</i>	0	0	0	0	0	0	0	0.5
<i>Chenopodium album</i>	0	0	0	0	0	0	0	0
<i>Cicuta bulbifera</i>	0	0	0	0	0	0	0	0
<i>Cirsium arvense</i>	0	0	0	0	0	0	0	0
<i>Crepis tectorum</i>	0	0	0	0	0	0	0	0
<i>Dracocephalum</i> sp.	0	0	0	0	0	0	0.333	0
<i>Epilobium glandulosum</i>	0	0	0	0	0	0.333	0	0
<i>Epilobium glandulosum</i>	0	0	0	0	0	0	0	0
<i>Fragaria</i> sp.	0	0	0	0	0	0	0	0
<i>Galeopsis tetrahit</i>	0.25	0	0	0	0	0	0	0
<i>Galium trifidum</i>	0	0	0	0	0	0	0.333	0.25
<i>Geum aleppicum</i>	0	0	0	0	0	0	0	0
<i>Hoedium</i> sp	0	0.25	0	0	0	0	0	0
<i>Juncus filiformis</i>	0	0	0	0	0	0	0	0
<i>Juncus alpinus</i>	0	0	0.333	0	0	0	0	0
<i>Juncus dudleyi</i>	0	0	0	0	0	0	0	0
<i>Juncus nodosus</i>	0	0	0	0	0	0	0	0
<i>Lycopus americanus</i>	0	0	0	0	0	0	0	0
<i>Mentha arvensis</i>	0	0	0	0.2	0.333	0.333	0.333	0.25
Mustard x	0	0	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0	0
<i>Poa palustris</i>	0.25	0.25	0	0.2	0	0.667	0	0
<i>Polygonum lapathifolium</i>	0.25	0	0	0.4	0	0	0	0
<i>Potentilla norvegica</i>	0.25	0.25	0.333	0.4	0	1	0.667	0.75
<i>Ranunculus sceleratus</i>	0.5	0.25	0.667	0.8	0.667	0	0	0.25
<i>Rorippa Islandica</i>	0	0.25	0.333	0.8	0.667	0.333	0	0.75
<i>Rumex maritimus</i>	0.25	0.25	0	0.6	0.333	0	0.333	0.25
<i>Setaria viridis</i>	0	0.25	0	0	0	0	0	0
<i>Sium suave</i>	0	0	0	0	0	0	0	0
<i>Solidago canadensis</i>	0	0	0	0	0	0	0	0
<i>Sonchus arvensis</i>	0	0	0	0	0	0	0	0
<i>Sonchus asper</i>	0	0	0	0	0	0	0.333	0
<i>Stachys palustris</i>	0	0.25	0	0	0.333	0	0	0
Stink	0.25	0	0	0	0	0	0	0
<i>Taraxacum officinale</i>	0	0	0.333	0	0	0.333	0	0
<i>Thlaspi arvense</i>	0	0.25	0	0	0	0	0	0
<i>Typha latifolia</i>	0.5	0	0	0.2	0	0	0	0
<i>Urtica dioica</i>	0.75	0.5	0.333	0.2	0.333	1	0	0.5
SPB	0	0	0	0	0	0	0	0
SPC	0	0	0	0	0	0	0	0
Grass X	0	0	0	0	0	0	0	0
<i>Carex p</i>	0	0	0	0	0	0	0	0
SPE	0	0	0	0	0	0	0	0
<i>Spirea</i> sp.	0	0	0	0	0	0	0	0

Appendix 2.4

Meadow	2	2	3	3	3	3	5	5
Transect	4	5	1	2	3	4	1	2
Species								
Agrostis scabra	0.25	0	0	0	0	0	0	0
Alopecurus aequalis	0	0	0	0	0	0	0	0
Amaranthus retroflexus	0	0	0.667	0.5	0.5	0	0	0
Aster simplex	0	0	0	0	0	0	0	0
Bidens cernua	0	0	0	0	0	0	0	0
Beckmannia syzigachne	0	0	0	0	0	0	0	0
Bromus inermis	0	0.25	0	0	0	0	0	0
Carex atherodes	0	0.25	0	0	0.5	0	0	0
Carex aquatilis	0	0	0	0	0.5	0	0	0.667
Carex sychnocephala	0.25	0	0	0	0	0	0	0
Carex rostrata	0	0	0	0	0	0	0	0
Chenopodium rubrum	0	0.25	0	0	0	0	0	0
Chenopodium album	0	0	0	0	0	0	0	0
Cicuta bulbifera	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	0	0	0	0
Crepis tectorum	0	0	0	0	0	0	0	0
Dracocephalum sp.	0	0	0	0.5	0	0	0	0
Epilobium glandulosum	0	0	0	0	0	0	0	0
Epilobium glandulosum	0	0	0	0	0	0	0	0
Fragaria sp.	0	0	0	0	0	0	0	0
Galeopsis tetrahit	0	0	0	0	0	0	0	0
Galium trifidum	0	0	0	0	0	0	0	0
Geum aleppicum	0	0	0	0	0	0	0	0
Hoedum sp	0	0	0	0	0	0	0	0
Juncus filiformis	0	0	0	0	0	0	0	0
Juncus alpinus	0	0	0	0	0	0	0	0
Juncus dudleyi	0	0	0	0	0	0	0	0
Juncus nodosus	0	0	0	0	0	0	0	0
Lycopus americanus	0	0	0	0	0	0	0	0
Mentha arvensis	0	0	0	0	0	0	0	0
Mustard x	0	0	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0	0
Poa palustris	0	0	0	0	0	0	0	0
Polygonum lapathifolium	0	0	0.333	0	0	0	0.333	0
Potentilla norvegica	0	0.5	0.333	0	0	0	0.333	0.333
Ranunculus sceleratus	0.5	0.5	0	1	0	0.5	0	0.333
Rorippa islandica	0	0.25	0.333	0	0	0	0	0
Rumex maritimus	0.75	0.75	0	0.5	0.5	0	0	0
Setaria viridis	0	0.25	0	0	0	0	0	0
Sium suave	0	0	0	0	0	0	0	0
Solidago canadensis	0	0	0	0	0	0	0	0
Sonchus arvensis	0	0	0	0	0	0	0	0
Sonchus asper	0	0	0.333	0	0	0	0	0
Stachys palustris	0	0	0.333	0	0	0	0	0
Stink	0	0	0.333	0	0	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0
Thlaspi arvense	0	0	0	0	0	0	0	0
Typha latifolia	0	0	0	0	0	0	0	0
Urtica dioica	0.5	0	0.667	0.5	0	0	0.667	0.667
SP B	0	0	0	0	0	0	0.667	0
SP C	0	0	0	0	0	0.5	0	0
Grass X	0	0	0	0	0	0	0	0
Carex p	0.25	0	0	0	0	0	0	0
SPE	0	0	0	0	0	0	0	0
Spirea sp.	0	0	0	0	0	0	0	0.333

Appendix 2.4

Meadow	5	5	7	7	7	7	8	8
Transect	3	4	1	2	3	4	1	2
Species								
Agrostis scabra	0	0	0	0	0	0	0	0
Alopecurus aequalis	0	0	0	0	0	0	0	0
Amaranthus retroflexus	0.5	1	0.333	0.25	0	0.667	0	0.2
Aster simplex	0	0	0	0	0	0	0.2	0
Bidens cernua	0	0	0	0	0	0	0	0
Beckmannia syzigachne	0	0	0	0	0	0.333	0	0.2
Bromus inermis	0	0	0	0	0	0	0	0.2
Carex atherodes	0	0	0	0	0	0	0	0
Carex aquatilis	0	0.333	0	0	0	0	0	0
Carex sychnocephala	0	0	0	0	0	0	0	0
Carex rostrata	0	0	0	0	0	0	0	0
Chenopodium rubrum	0	0	0	0	0.333	0	0	0
Chenopodium album	0	0	0	0.25	0.333	0	0	0
Cicuta bulbifera	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0.333	0	0	0.333	0	0
Crepis tectorum	0	0	0	0	0	0	0	0
Dracocephalum sp.	0	0	0	0.25	0	0	0.2	0
Epilobium glandulosum	0	0	0.333	0	0	0	0	0.2
Epilobium glandulosum	0	0	0	0	0	0	0	0.2
Fragaria sp.	0	0	0	0	0	0	0	0
Galeopsis tetrahit	0	0	0	0	0	0	0	0
Galium trifidum	0	0.333	0	0	0	0	0	0
Geum aleppicum	0	0	0	0	0	0	0	0
Hoedum sp	0	0	0	0	0	0	0	0
Juncus filiformis	0	0	0	0	0	0	0	0
Juncus alpinus	0	0	0	0	0	0	0	0
Juncus dudleyi	0	0	0	0	0	0	0	0
Juncus nodosus	0	0	0	0	0	0	0	0
Lycopus americanus	0	0	0	0	0	0	0.2	0
Mentha arvensis	0.5	0.333	0	0.25	0.333	0	0	0.2
Mustard x	0	0.333	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0	0
Poa palustris	0	0	0	0.25	0	0.333	0.2	0
Polygonum lapathifolium	0	0	0	0	0	0	0	0
Potentilla norvegica	0	0.333	0	0.25	0.333	0.333	0.2	0.2
Ranunculus sceleratus	0.5	0	0	0.25	0	0	0	0.4
Rorippa islandica	0	0.333	0	0	0	0	0.2	0.2
Rumex maritimus	0	0.333	0	0	0	0	0.2	0
Setaria viridis	0	0	0	0	0	0	0	0
Sium suave	0	0	0	0	0	0	0	0
Solidago canadensis	0	0	0	0	0	0	0	0.2
Sonchus arvensis	0	0	0	0	0.333	0	0	0
Sonchus asper	0	0	0	0	0	0	0	0
Stachys palustris	0	0	0	0	0	0	0	0
Stink	0	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0
Thlaspi arvense	0	0	0	0	0	0	0	0
Typha latifolia	0	0	0	0	0	0	0	0
Urtica dioica	0.5	0.333	1	0.5	0.667	0.333	0.6	0.4
SP B	0	0	0	0	0	0	0	0
SP C	0	0	0	0	0	0	0	0
Grass X	0	0	0.333	0	0	0	0	0
Carex p	0	0	0	0	0	0	0	0
SPE	0	0	0	0	0	0	0	0
Spiraea sp.	0	0	0	0	0	0	0	0

Appendix 2.4

Meadow	8	8	8	11	11	11	11	12
Transect	3	4	5	1	2	3	4	1
Species								
<i>Agrostis scabra</i>	0	0	0	0	0	0	0	0
<i>Alopecurus aequalis</i>	0	0	0	0	0	0	0	0
<i>Amaranthus retroflexus</i>	0.5	0.667	0.333	0.5	0.167	0.25	0.25	0.75
<i>Aster simplex</i>	0	0	0	0	0	0	0	0
<i>Bidens cernua</i>	0	0	0	0.25	0	0	0	0
<i>Beckmannia syzigachne</i>	0	0	0	0	0	0	0.25	0
<i>Bromus inermis</i>	0	0	0	0	0	0	0	0
<i>Carex atherodes</i>	0	0	0	0	0	0	0	0
<i>Carex aquatilis</i>	0	0	0	0	0	0	0.25	0
<i>Carex sychnocephala</i>	0	0	0	0	0	0	0	0
<i>Carex rostrata</i>	0	0	0	0	0	0	0	0
<i>Chenopodium rubrum</i>	0	0	0	0	0	0	0	0
<i>Chenopodium album</i>	0	0	0	0	0	0	0	0.25
<i>Cicuta bulbifera</i>	0	0	0	0	0	0	0	0
<i>Cirsium arvense</i>	0	0	0	0	0.167	0	0.25	0
<i>Crepis tectorum</i>	0	0	0	0	0	0	0	0
<i>Dracocephalum</i> sp.	0.25	0	0	0	0	0	0	0
<i>Epilobium glandulosum</i>	0.25	0.333	0	0	0.167	0	0.25	0.25
<i>Epilobium glandulosum</i>	0	0	0	0	0	0	0	0
<i>Fragaria</i> sp.	0	0.333	0	0	0	0	0	0
<i>Galeopsis tetrahit</i>	0	0	0	0	0	0	0	0
<i>Galium trifidum</i>	0	0.333	0	0	0	0.25	0	0
<i>Geum aleppicum</i>	0	0	0.333	0	0	0	0	0
<i>Hoedum</i> sp.	0	0	0	0	0	0	0	0
<i>Juncus filiformis</i>	0	0.333	0	0	0	0	0	0
<i>Juncus alpinus</i>	0	0	0	0	0	0	0	0
<i>Juncus dudleyi</i>	0	0	0	0	0.167	0	0	0
<i>Juncus nodosus</i>	0	0	0	0	0.167	0	0	0
<i>Lycopus americanus</i>	0	0	0	0	0	0	0	0
<i>Mentha arvensis</i>	0	0.333	0.333	0	0.333	0	0.25	0
Mustard x	0	0	0	0	0	0	0.25	0
plant x	0	0	0	0	0	0	0	0
<i>Poa palustris</i>	0	0	0	0.5	0	0	0.5	0.25
<i>Polygonum lapathifolium</i>	0	0	0	0	0.167	0	0	0
<i>Potentilla norvegica</i>	0.25	0.667	0	0.5	0.167	0.75	0.5	0.25
<i>Ranunculus sceleratus</i>	0.5	0.667	0	0.25	0.167	0.25	0.25	0
<i>Rorippa islandica</i>	0	0.333	0	0	0.667	0.25	1	0.25
<i>Rumex maritimus</i>	0.25	0.333	0.333	0.25	0.5	0	0	0.25
<i>Setaria viridis</i>	0.25	0	0	0	0.167	0	0	0
<i>Sium suave</i>	0	0	0	0	0	0	0	0
<i>Solidago canadensis</i>	0	0	0	0	0	0	0	0
<i>Sonchus arvensis</i>	0	0	0	0	0	0	0	0
<i>Sonchus asper</i>	0	0	0	0	0	0	0	0
<i>Stachys palustris</i>	0	0	0	0	0	0	0	0
Stink	0	0.667	0	0	0.167	0	0	0
<i>Taraxacum officinale</i>	0	0	0	0	0	0	0	0
<i>Thlaspi arvense</i>	0	0	0	0	0	0	0	0
<i>Typha latifolia</i>	0	0	0	0	0	0	0	0
<i>Urtica dioica</i>	0.25	0.333	0.333	0	0.167	0	0.5	0.25
SP B	0	0	0	0	0	0	0	0
SP C	0	0	0	0	0	0	0	0
Grass X	0	0	0	0	0	0	0	0
<i>Carex</i> p	0	0	0	0	0	0	0	0
SPE	0.25	0	0	0	0	0	0	0
<i>Spirea</i> sp.	0	0	0	0	0	0	0	0

Appendix 2.4

Meadow	12	12	12	14	14	14	14	15
Transect	2	3	4	1	2	3	4	1
Species								
<i>Agrostis scabra</i>	0	0	0	0	0	0	0	0
<i>Alopecurus aequalis</i>	0	0	0	0	0	0	0.333	0
<i>Amaranthus retroflexus</i>	0.25	0.5	0	0.333	0.333	0.333	0	0
<i>Aster simplex</i>	0	0	0	0	0	0	0	0
<i>Bidens cernua</i>	0	0	0.333	0	0.333	0	0	0
<i>Beckmannia syzigachne</i>	0	0	0.333	0	0	0	0	0
<i>Bromus inermis</i>	0	0	0	0.333	0	0	0	0
<i>Carex atherodes</i>	0	0	0	0	0	0	0	0
<i>Carex aquatilis</i>	0.5	0	0	0	0	0	0.333	0
<i>Carex sychnocephala</i>	0	0.5	0	0	0	0	0	0
<i>Carex rostrata</i>	0	0	0	0	0	0	0	0
<i>Chenopodium rubrum</i>	0.25	0	0	0	0.333	0.333	0	0
<i>Chenopodium album</i>	0	0	0	0	0	0	0	0
<i>Cicuta bulbifera</i>	0	0.5	0	0	0	0	0	0
<i>Cirsium arvense</i>	0	0	0	0	0	0	0	0
<i>Crepis tectorum</i>	0	0	0	0	0	0.333	0	0
<i>Dracocephalum</i> sp.	0	0	0	0	0	0	0	0
<i>Epilobium glandulosum</i>	0	1	0.333	0	0	0.333	0	0
<i>Epilobium glandulosum</i>	0	0	0	0	0	0	0	0
<i>Fragaria</i> sp.	0	0	0.333	0	0.333	0	0	0
<i>Galeopsis tetrahit</i>	0	0	0	0	0	0	0	0
<i>Galium trifidum</i>	0	0	0.333	0	0	0.667	0	0
<i>Geum aleppicum</i>	0	0.5	0	0	0	0	0	0
<i>Hoedum</i> sp	0	0	0	0	0	0	0	0
<i>Juncus filiformis</i>	0	0	0	0	0	0	0	0
<i>Juncus alpinus</i>	0.25	0	0	0	0	0	0	0
<i>Juncus dudleyi</i>	0	0	0	0	0	0	0	0
<i>Juncus nodosus</i>	0.25	0.5	0	0	0	0.333	0	0
<i>Lycopus americanus</i>	0	0	0	0	0	0	0	0
<i>Mentha arvensis</i>	0	0	0.667	0	0	0.333	0.333	0
Mustard x	0	0	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0	0
<i>Poa palustris</i>	0	0	0	0	0	0	0	0.25
<i>Polygonum lapathifolium</i>	0	0	0	0	0	0	0	0
<i>Potentilla norvegica</i>	1	1	0.667	0	0.333	0.667	0	0.25
<i>Ranunculus sceleratus</i>	0.25	1	0.667	0	0	0.333	0.333	0
<i>Rorippa islandica</i>	0.5	1	0.667	0	0	0	0.333	0
<i>Rumex maritimus</i>	0	0	0	0	0.667	0.667	0.333	0.25
<i>Setaria viridis</i>	0	0	0	0	0	0	0	0
<i>Slum suave</i>	0	0	0.333	0	0	0	0	0.25
<i>Solidago canadensis</i>	0	0	0	0	0	0	0	0
<i>Sonchus arvensis</i>	0	0	0	0	0	0	0	0
<i>Sonchus asper</i>	0	0	0	0	0	0	0	0
<i>Stachys palustris</i>	0	0	0	0	0	0	0	0
Stink	0.25	0.5	0	0.333	0	0.333	0	0
<i>Taraxacum officinale</i>	0	0	0	0	0	0	0	0
<i>Thlaspi arvense</i>	0	0	0	0	0	0	0	0
<i>Typha latifolia</i>	0	0	0	0	0	0	0	0.25
<i>Urtica dioica</i>	0	0	0.333	0.333	0.333	0	0.667	0.25
SPB	0	0	0	0	0	0	0	0
SPC	0	0	0	0.333	0	0	0	0
Grass X	0	0	0	0	0	0	0	0
<i>Carex</i> p	0.25	0	0	0	0	0	0	0
SPE	0	0	0	0	0	0	0	0
<i>Spirea</i> sp.	0	0	0	0	0	0	0	0

Appendix 2.4

Meadow	15	15	15	p4	p4	p4	p4
Transect	2	3	4	1	2	3	4
Species							
Agrostis scabra	0.25	0	0	0	0	0	0
Alopecurus aequalis	0	0	0	0	0	0	0
Amaranthus retroflexus	0.5	0.25	0.75	0	0.5	0	0.667
Aster simplex	0	0	0	0	0	0	0
Bidens cernua	0	0	0	0	0	0	0
Beckmannia syzigachne	0	0.25	0.5	0	0	0	0
Bromus inermis	0	0	0	0	0	0	0
Carex atherodes	0	0	0	0	0	0	0.333
Carex aquatilis	0	0	0	0	0.25	0	0
Carex sychnocephala	0	0	0	0	0	0	0
Carex rostrata	0	0	0	0	0	0	0
Chenopodium rubrum	0	0	0	0	0	0	0
Chenopodium album	0	0	0	0.333	0	0	0
Cicuta bulbifera	0	0	0	0	0	0	0
Cirsium arvense	0	0	0.25	0	0	0	0.333
Crepis tectorum	0	0	0	0	0	0	0
Dracocephalum sp.	0	0	0	0	0	0.333	0
Epilobium glandulosum	0.25	0.5	0.25	0	0	0	0
Epilobium glandulosum	0	0	0.25	0	0	0	0
Fragaria sp.	0	0	0	0	0	0	0
Galeopsis tetrahit	0	0	0	0	0	0	0
Gallium trifidum	0	0	0.25	0	0.25	0	0.333
Geum aleppicum	0	0	0	0	0	0	0
Hoedum sp	0	0	0	0	0	0	0
Juncus filiformis	0	0	0	0	0	0	0
Juncus alpinus	0	0	0	0	0	0	0
Juncus dudleyi	0.25	0	0	0	0	0	0
Juncus nodosus	0	0	0	0	0	0	0
Lycopus americanus	0	0	0.25	0	0	0	0
Mentha arvensis	0.25	0	0	1	0	0.333	0.333
Mustard x	0	0	0	0	0	0	0
plant x	0	0	0	0.333	0	0	0
Poa palustris	0	0	0.25	0.333	0.25	0.667	0
Polygonum lapathifolium	0	0	0	0	0	0	0.333
Potentilla norvegica	0.5	0	0.5	0	0.25	0.333	0.333
Ranunculus sceleratus	0	0.75	0.25	0.333	0	0.333	0.333
Rorippa islandica	0.5	0	0.5	0	0	0	0
Rumex maritimus	0.25	0.25	0.25	0	0	0	0
Setaria viridis	0	0.25	0	0	0.25	0	0
Sium suave	0	0	0	0	0.25	0	0
Solidago canadensis	0	0	0	0.333	0	0	0
Sonchus arvensis	0	0	0	0	0	0	0
Sonchus asper	0	0	0	0	0	0	0
Stachys palustris	0	0	0	0	0	0	0
Stink	0	0.25	0	0	0	0	0.333
Taraxacum officinale	0	0	0	0	0	0	0
Thlaspi arvense	0	0	0	0	0	0	0
Typha latifolia	0	0.25	0	0	0	0	0
Urtica dioica	0.25	0	0	1	0.75	0.333	0.333
SP B	0	0	0	0	0	0	0
SP C	0	0	0	0	0	0	0
Grass X	0	0	0	0	0	0	0
Carex p	0	0.25	0	0	0	0	0
SP E	0	0	0	0	0	0	0
Spirea sp.	0	0	0	0	0	0	0

Appendix 2.5 Species seed frequencies in the non cold treated meadow samples

Meadow	1	1	1	1	1	2	2	2	2	2
Transect	1	2	3	4	5	1	2	3	4	5
Species										
Agrostis scabra	0	0.25	0	0.2	0	0	0	0	0	0
Alopecurus aequalis	0	0	0	0	0	0	0	0	0	0
Amaranthus retroflexus	0	0	0	0	0	0	0	0	0	0
Amaranthus retroflexus	0	0	0	0	0	0	0	0	0	0
Anemone canadensis	0	0	0	0	0	0	0	0	0	0
Beckmannia syzigachne	0	0	0	0	0	0	0.333	0.25	0	0
Bidens cernua	0	0	0	0	0	0	0	0	0	0
Bromus inermis	0	0	0	0	0	0	0	0	0	0
Calamagrostis canadensis	0	0	0	0	0	0	0	0	0	0
Carex atherodes	0	0	0	0	0.333	0	0	0	0.25	0
Carex aquatilis	0	0	0	0	0	0	0	0.25	0	0
Carex rostrata	0	0	0.333	0	0	0	0	0	0.25	0
Carex sychrocephala	0	0	0	0	0	0	0	0	0	0
Carex q	0	0	0	0	0	0	0	0	0	0
Carex sspatosis	0	0	0	0	0	0	0	0	0	0
Chenopodium rubrum	0	0	0	0	0	0	0.667	0.25	0.5	0.25
Chenopodium album	0	0	0	0	0	0	0	0	0	0
Cicuta bulbifera	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	0	0.333	0.667	0.25	0	0
Dracocephalum sp.	0	0	0	0	0	0	0	0	0	0
Eleocharis sp.	0	0	0	0	0	0	0	0	0	0
Epilobium glandulosum	0.25	0	0	0	0.333	0	0	0	0.25	0
Galeopsis tetrahit	0.25	0	0	0	0	0	0	0	0	0
Galium trifidum	0	0.25	0	0	0	0	0.333	0	0	0
Geum aleppicum	0	0	0	0	0	0	0	0	0	0
Geum Macrophyllum	0	0	0	0	0.667	0	0	0	0	0
Glyceria striata	0	0	0.333	0.2	0	0	0.667	0.25	0.25	0
grass y	0	0	0	0	0	0	0	0	0	0
Juncus alpinus	0	0	0	0	0	0	0	0	0	0
Juncus dudleyi	0	0	0	0	0	0	0	0	0	0
Juncus nodosus	0	0	0	0	0	0	0	0	0	0
Lycopus uniflorus	0	0	0	0	0	0	0	0	0	0
Lycopus americanus	0	0	0	0	0	0	0	0	0	0
Menthe arvensis	0	0	0	0.4	0.333	0	0	0	0	0
Mint x	0	0	0	0	0	0	0	0	0	0
Mustard x	0	0	0	0	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0	0	0	0
Plantago major	0	0	0	0	0	0	0	0	0	0
Poa palustris	1	0.5	0.333	0.6	0.667	0.333	0	0	0.5	0
Poa trivialis	0.25	0	0	0	0	0	0	0	0	0
Polygonum amphibium	0.25	0	0	0.2	0	0	0.333	0	0	0
Polygonum lapathifolium	0	0	0	0	0	0	0	0	0	0
Potentilla norvegica	0.5	0.25	0	0.6	0.333	0.333	1	0.25	0.25	0.25
Ranunculus sceleratus	0.75	0.75	1	0.6	0.667	0.333	0.667	0.25	0.75	0.5
Rorripa islandica	0.5	0.25	1	0.6	1	0	0.333	0.25	0	0
Rumex maritimus	0.25	0.75	0.333	0.8	0.667	0	0.667	0.25	0.5	0.25
Scutellaria galericulata	0	0	0	0	0	0	0	0	0	0
Setaria vividis	0	0	0	0	0	0	0	0	0	0
Sium suave	0	0	0	0	0.333	0	0	0	0	0
Solidago canadensis var c	0	0	0	0	0.333	0	0	0	0	0
Sonchus arvensis	0	0.25	0	0	0	0.667	0.667	0.25	0	0
Stachys palustris	0	0	0	0	0	0	0	0	0	0
Stellaria crassifolia	0	0	0	0	0	0	0	0	0	0
Stink	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0
Thlaspi arvense	0	0	0	0	0	0	0	0	0	0
Typha latifolia	0	0	0	0	0	0	0	0	0	0
Urtica dioica	0.25	0.25	0	0.4	0.333	0.667	0.667	0.25	0.25	0
Vicia americana	0	0	0	0	0	0	0	0	0	0
Species e	0	0	0	0	0	0	0	0	0	0
Species f	0	0	0	0	0	0	0	0	0	0
Species q	0	0	0	0	0	0	0	0	0	0

Appendix 2.5

Meadow	3	3	3	3	5	5	5	5	7	7
Transect	1	2	3	4	1	2	3	4	1	2
Species										
<i>Agrostis scabra</i>	0	0	0	0	0	0	0	0	0.333	0
<i>Alopecurus aequalis</i>	0	0	0	0	0	0	0	0	0	0
<i>Amaranthus retroflexus</i>	0	0	0	0	0	0	0	0	0	0
<i>Amaranthus retroflexus</i>	0	0	0	0	0	0	0	0	0	0
<i>Anemone canadensis</i>	0	0	0	0	0.333	0	0	0	0	0
<i>Beckmannia syzigachne</i>	0	0	0	0	0	0	0	0	0	0
<i>Bidens cernua</i>	0	0	0	0	0	0	0	0	0	0
<i>Bromus inermis</i>	0	0	0	0	0	0	0	0	0	0
<i>Calamagrostis canadensis</i>	0	0	0	0	0	0	0	0	0	0
<i>Carex atherodes</i>	0	0	0	0	0	0.25	0	0	0	0
<i>Carex aquatilis</i>	0	0	0	0	0.333	0	0	0	0	0
<i>Carex rostrata</i>	0	0	0	0	0	0	0	0	0	0
<i>Carex sychrocephala</i>	0	0	0	0	0	0	0	0	0	0
<i>Carex q</i>	0	0	0	0.5	0	0	0	0	0	0
<i>Carex sespatosis</i>	0.333	0	0	0	0	0	0	0	0	0
<i>Chenopodium rubrum</i>	0	0.5	1	0	0	0.25	0	0	0	0.25
<i>Chenopodium album</i>	0	0	0	0	0	0	0	0	0	0
<i>Cicuta bulbifera</i>	0	0	0	0	0	0	0	0	0	0
<i>Cirsium arvense</i>	0	0	0	0	0.333	0	0	0	0	0
<i>Dracocephalum sp.</i>	0	0	0	0	0	0	0	0	0	0
<i>Eleocharis sp.</i>	0	0	0	0	0	0	0	0	0	0
<i>Epilobium glandulosum</i>	0	0	0	0	0	0	0	0.333	0	0
<i>Galeopsis tetrahit</i>	0.333	0	0	0	0	0	0	0	0	0
<i>Galium trifidum</i>	0	0	0.5	0	0	0.25	0	0.333	0	0
<i>Geum aleppicum</i>	0	0	0	0	0	0	0	0	0	0
<i>Geum Macrophyllum</i>	0	0	0	0	0	0	0	0	0	0
<i>Glyceria striata</i>	0	1	0.5	0.5	0	0.25	0	0	0	0
grass y	0	0	0	0	0	0	0	0	0	0
<i>Juncus alpinus</i>	0	0	0	0	0	0	0	0.333	0	0
<i>Juncus dudleyi</i>	0	0	0	0	0	0	0	0	0	0
<i>Juncus nodosus</i>	0	0	0	0	0	0	0	0	0	0
<i>Lycopus uniflorus</i>	0	0	0	0	0	0	0	0	0	0
<i>Lycopus americanus</i>	0	0	0	0	0	0	0	0	0	0
<i>Menthe arvensis</i>	0	0.5	0	0	0	0.25	0.5	0.333	0	0.5
Mint x	0	0	0	0	0	0	0	0	0	0
Mustard x	0	0	0	0	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0	0	0	0
<i>Plantago major</i>	0	0	0	0	0	0	0	0.333	0	0
<i>Poa palustris</i>	0.333	0	0.5	0.5	0.333	0.5	0	0	0.333	0.25
<i>Poa trivialis</i>	0	0	0	0	0	0	0	0	0	0
<i>Polygonum amphibium</i>	0	0	0	0	0	0	0	0.333	0	0
<i>Polygonum lapathifolium</i>	0	0	0	0	0	0	0	0	0	0
<i>Potentilla norvegica</i>	0.333	0.5	0	0	0	0.25	0.5	0.667	0	0.5
<i>Ranunculus sceleratus</i>	0.667	0.5	1	0.5	0.333	0.5	0	0	0	0
<i>Rorripa islandica</i>	0	0	0	0	0	0.25	0	0.333	0	0
<i>Rumex maritimus</i>	0	0.5	0.5	0.5	0	0.25	0	0.333	0	0
<i>Scutellaria galericulata</i>	0	0	0	0	0.333	0	0	0	0	0
<i>Setaria vividis</i>	0	0	0	0	0	0	0	0	0	0
<i>Sium suave</i>	0	0	0	0	0	0.25	0	0	0	0
<i>Solidago canadensis var c</i>	0	0	0	0	0	0	0	0	0	0
<i>Sonchus arvensis</i>	0	0	0	0	0	0	0	0	0	0
<i>Stachys palustris</i>	0	0	0	0	0	0	0	0	0	0
<i>Stellaria crassifolia</i>	0	0	0.5	0	0	0	0	0	0	0
Stink	0	0	0	0	0	0	0	0	0	0
<i>Taraxacum officinale</i>	0	0	0	0	0	0	0	0	0	0
<i>Thlaspi arvense</i>	0	0	0	0	0	0	0	0	0	0
<i>Typha latifolia</i>	0	0	0	0	0	0	0	0	0	0
<i>Urtica dioica</i>	1	1	0.5	1	0.667	0.5	0.5	0.667	0.333	0.25
<i>Vicia americana</i>	0	0	0	0	0	0	0	0	0	0
Species e	0	0	0	0	0.333	0	0	0	0	0
Species f	0	0	0	0	0	0	0	0	0	0.25
Species q	0	0	0	0	0	0	0	0	0	0

Appendix 2.5

Meadow	7	7	8	8	8	8	8	11	11	11
Transect	3	4	1	2	3	4	5	1	2	3
Species										
Agrostis scabra	0	0	0	0	0	0	0	0	0	0
Alopecurus aequalis	0	0	0	0	0	0	0	0	0	0
Amaranthus retroflexus	0	0	0	0	0	0	0	0	0	0
Amaranthus retroflexus	0	0	0	0	0	0	0	0	0	0
Anemone canadensis	0	0	0	0	0	0	0	0	0	0
Beckmannia syzigachne	0	0	0	0	0	0	0	0	0	0
Bidens cernua	0	0	0.2	0	0.25	0	0	0	0	0
Bromus inermis	0	0	0	0	0	0	0	0	0	0
Calamagrostis canadensis	0	0	0	0	0	0	0	0.25	0	0
Carex atherodes	0.333	0	0	0.2	0	0	0	0	0.167	0
Carex aquatilis	0	0	0	0	0	0	0	0.25	0	0
Carex rostrata	0	0	0	0	0	0.333	0	0	0.167	0
Carex sychrocephala	0	0	0	0	0	0	0	0	0	0
Carex q	0	0	0	0	0	0	0	0	0	0
Carex sspatosis	0	0	0	0.2	0	0	0	0.25	0	0
Chenopodium rubrum	0.333	0	0	0	0	0	0	0	0	0
Chenopodium album	0	0	0	0	0	0	0	0	0	0
Cicuta bulbifera	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	0	0.333	0	0	0	0	0	0.25	0	0
Dracocephalum sp.	0	0	0	0	0	0	0	0	0	0
Eleocharis sp.	0	0	0	0.2	0	0	0	0	0	0
Epilobium glandulosum	0	0	0	0.4	0	1	0	0	0	0.25
Galeopsis tetrahit	0	0	0	0	0	0.333	0	0	0	0
Galium trifidum	0	0	0.2	0	0	0.333	0	0	0	0.25
Geum aleppicum	0	0	0	0	0	0	0	0	0	0
Geum Macrophyllum	0	0	0	0	0	0	0	0	0	0
Glyceria striata	0	0.333	0	0	0.25	0	0	0.25	0.5	0.25
grass y	0	0	0	0	0.25	0	0	0	0	0
Juncus alpinus	0	0	0	0	0	0	0	0	0	0
Juncus dudleyi	0	0	0	0	0	0	0	0	0	0
Juncus nodosus	0	0	0	0	0	0	0	0	0	0
Lycopus uniflorus	0	0	0	0	0	0	0	0	0	0.25
Lycopus americanus	0	0	0	0	0	0	0	0	0	0
Menthe arvensis	0	0.333	0	0	0	0.333	0	0	0.167	0
Mint x	0	0	0	0	0	0	0	0	0	0
Mustard x	0	0	0	0	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0	0	0	0
Plantago major	0	0	0	0	0	0	0	0	0.167	0
Poa palustris	0	0.667	0.4	0.6	0.5	0.333	0.333	0.25	0.333	0.25
Poa trivialis	0	0	0	0	0	0	0	0	0	0
Polygonum amphibium	0	0	0	0	0.25	0	0	0	0	0
Polygonum lapathifolium	0	0	0	0	0	0	0	0	0	0
Potentilla norvegica	0.333	0	0	0.2	0.25	0.667	0	0.25	0	0.25
Ranunculus sceleratus	0.333	0.333	0.4	0.2	0.5	0.667	0.333	0	0	0.25
Rorripa islandica	0	0	0	0.2	0	1	0	0	0.333	0.5
Rumex maritimus	0	0	0	0.2	0.25	0.333	0	0	0.833	0.5
Scutellaria galericulata	0	0	0	0	0	0	0	0	0	0
Setaria vividis	0	0	0	0	0	0	0	0	0	0
Sium suave	0	0.333	0	0	0	0	0	0	0	0
Solidago canadensis var c	0	0	0	0	0	0	0	0	0	0
Sonchus arvensis	0	0	0.2	0	0	0	0	0	0.167	0
Stachys palustris	0	0	0	0	0	0.333	0	0	0	0
Stellaria crassifolia	0	0	0	0	0	0.333	0	0	0	0
Stink	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0
Thlaspi arvense	0	0	0	0	0	0	0	0	0	0
Typha latifolia	0	0	0	0.2	0	0	0	0	0	0
Urtica dioica	0	0.667	0.6	0.4	0.25	0.667	0	0.5	0.167	0.25
Vicia americana	0	0	0	0	0	0	0	0	0	0
Species e	0	0	0	0	0	0	0	0	0	0
Species f	0	0	0	0	0	0	0	0	0	0
Species q	0	0	0	0	0	0.333	0	0	0	0

Appendix 2.5

Meadow	11	12	12	12	12	14	14	14	14	15
Transect	4	1	2	3	4	1	2	3	4	1
Species										
<i>Agrostis scabra</i>	0	0	0	0	0	0	0.333	0	0.333	0
<i>Alopecurus aequalis</i>	0	0	0	0	0	0	0	0	0	0
<i>Amaranthus retroflexus</i>	0	0	0	0	0	0	0	0	0	0
<i>Amaranthus retroflexus</i>	0	0	0	0	0	0	0	0	0	0
<i>Anemone canadensis</i>	0	0	0	0	0	0	0	0	0	0
<i>Beckmannia syzigachne</i>	0	0	0	0	0.333	0	0	0	0	0
<i>Bidens cernua</i>	0	0	0	0	0	0.333	0	0	0.333	0
<i>Bromus inermis</i>	0	0	0	0	0	0	0	0	0	0
<i>Calamagrostis canadensis</i>	0	0	0	0	0	0	0	0	0	0
<i>Carex atherodes</i>	0	0	0	0.5	0	0	0.333	0	0.333	0
<i>Carex aquatilis</i>	0	0.25	0	0	0	0	0	0	0	0
<i>Carex rostrata</i>	0	0	0.25	0	0	0	0	0	0	0
<i>Carex sychrocephala</i>	0	0	0	0.5	0	0	0	0	0	0
<i>Carex q</i>	0	0	0	0	0	0	0	0	0	0
<i>Carex sespatosis</i>	0	0	0	0	0.333	0	0	0	0	0
<i>Chenopodium rubrum</i>	0	0	0.25	0	0	0	0.333	0.333	0.333	0
<i>Chenopodium album</i>	0	0	0	0	0	0	0	0	0	0
<i>Cicuta bulbifera</i>	0	0	0	0	0	0	0	0	0	0
<i>Cirsium arvense</i>	0	0.25	0	0	0	0	0	0	0	0.25
<i>Dracocephalum sp.</i>	0	0	0	0	0	0	0	0	0	0
<i>Eleocharis sp.</i>	0	0	0	0	0	0	0	0	0	0
<i>Epilobium glandulosum</i>	0	0.25	0.25	0.5	0.333	0	0	0	0	0
<i>Galeopsis tetrahit</i>	0.25	0	0	0	0	0	0	0	0	0
<i>Galium trifidum</i>	0.25	0	0	0	0.667	0	0	0	0.333	0
<i>Geum aleppicum</i>	0	0	0	0	0	0	0	0	0	0
<i>Geum Macrophyllum</i>	0	0	0	0	0	0	0	0	0	0
<i>Glyceria striata</i>	0.25	0	0	0	0	0	0.667	0.667	0.667	0
grass y	0	0	0	0	0	0.333	0	0	0	0
<i>Juncus alpinus</i>	0	0	0	0	0	0	0	0	0	0
<i>Juncus dudleyi</i>	0	0	0	0	0	0	0	0	0	0
<i>Juncus nodosus</i>	0	0	0	0	0	0	0	0	0	0
<i>Lycopus uniflorus</i>	0.25	0	0	0	0	0	0	0	0	0
<i>Lycopus americanus</i>	0	0	0	0	0	0	0	0	0	0
<i>Menthe arvensis</i>	0.75	0	0	0.5	0.333	0	0	0.333	0.333	0
Mint x	0	0	0	0	0	0	0	0	0	0
Mustard x	0	0	0	0	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0	0	0	0
<i>Plantago major</i>	0	0	0	0	0	0	0	0.333	0	0
<i>Poa palustris</i>	0.5	0.5	0.25	0	0	0.333	0	0	0	0
<i>Poa trivialis</i>	0	0	0	0	0	0	0	0	0	0
<i>Polygonum amphibium</i>	0	0.25	0.25	0	0	0	0	0.333	0	0
<i>Polygonum lapathifolium</i>	0	0	0	0	0	0	0	0	0	0
<i>Potentilla norvegica</i>	0.5	0.25	1	1	1	0	0	0.333	0	0.5
<i>Ranunculus sceleratus</i>	0	0.25	0	0.5	0.667	0	0	0	0	0
<i>Rorripa islandica</i>	0.5	0.75	0.25	0.5	0.667	0	0	0.667	0.333	0
<i>Rumex maritimus</i>	0.25	0.5	0.25	0	0.333	0	0.667	0.333	0.667	0.25
<i>Scutellaria galericulata</i>	0	0	0	0	0	0	0	0	0	0
<i>Setaria vividis</i>	0	0	0	0	0	0	0	0	0	0
<i>Sium suave</i>	0.25	0	0	0	0	0	0	0	0	0
<i>Solidago canadensis</i> var c	0	0	0	0	0	0	0	0	0	0
<i>Sonchus arvensis</i>	0	0	0	0	0	0	0	0	0	0
<i>Stachys palustris</i>	0	0	0	0	0	0	0	0	0	0
<i>Stellaria crassifolia</i>	0	0	0	0	0	0	0	0	0	0
Stink	0	0	0	0	0	0	0	0	0	0
<i>Taraxacum officinale</i>	0	0	0	0	0	0	0	0	0	0
<i>Thlaspi arvense</i>	0	0	0	0	0	0	0	0	0	0
<i>Typha latifolia</i>	0	0	0	0	0	0	0	0	0	0
<i>Urtica dioica</i>	0.75	0.25	0.25	0	0.667	0.333	0.333	0.333	0.667	0.25
<i>Vicia americana</i>	0	0	0	0	0	0.333	0	0	0	0
Species e	0	0	0	0	0	0	0	0	0	0
Species f	0	0	0	0	0	0	0	0	0	0
Species q	0	0	0	0	0	0	0	0	0	0

Appendix 2.5

Meadow	15	15	15	p4	p4	p4	p4
Transect	2	3	4	1	2	3	4
Species							
<i>Agrostis scabra</i>	0	0	0	0.333	0	0	0
<i>Alopecurus aequalis</i>	0	0	0	0	0	0	0
<i>Amaranthus retroflexus</i>	0	0	0	0	0	0	0
<i>Amaranthus retroflexus</i>	0	0	0	0	0	0	0
<i>Anemone canadensis</i>	0	0	0	0	0	0	0
<i>Beckmannia syzigachne</i>	0.25	0	0.25	0	0	0	0
<i>Bidens cernua</i>	0	0	0	0	0.25	0	0
<i>Bromus inermis</i>	0	0	0	0	0	0	0
<i>Calamagrostis canadensis</i>	0	0	0	0	0	0	0
<i>Carex atherodes</i>	0	0	0	0	0	0.333	0
<i>Carex aquatilis</i>	0	0	0	0	0	0	0
<i>Carex rostrata</i>	0	0	0	0	0	0	0
<i>Carex sychrocephala</i>	0	0	0	0	0	0	0
<i>Carex q</i>	0	0	0	0	0	0	0
<i>Carex sspatosis</i>	0	0	0.5	0	0	0	0.333
<i>Chenopodium rubrum</i>	0.25	0	0	0	0	0	0
<i>Chenopodium album</i>	0	0	0	0	0	0	0
<i>Cicuta bulbifera</i>	0	0	0	0	0	0	0
<i>Cirsium arvense</i>	0.25	0	0.25	0	0	0.333	0.333
<i>Dracocephalum sp.</i>	0	0	0	0	0	0	0
<i>Eleocharis sp.</i>	0	0	0	0	0	0	0
<i>Epilobium glandulosum</i>	0	0.25	0	0.333	0	0.333	0
<i>Galeopsis tetrahit</i>	0	0	0	0	0	0	0
<i>Galium trifidum</i>	0	0.25	0.25	0	0	0.333	0.333
<i>Geum aleppicum</i>	0	0	0	0	0	0	0
<i>Geum Macrophyllum</i>	0	0	0.25	0	0	0	0
<i>Glyceria striata</i>	0.25	0.25	0.25	0.333	0	0	0
grass y	0	0	0	0	0	0	0
<i>Juncus alpinus</i>	0	0	0	0	0	0	0
<i>Juncus dudleyi</i>	0	0	0	0	0	0	0
<i>Juncus nodosus</i>	0	0	0	0	0	0	0
<i>Lycopus uniflorus</i>	0	0	0	0	0	0	0
<i>Lycopus americanus</i>	0	0	0	0	0	0	0
<i>Menthe arvensis</i>	0.25	0	0	0.333	0	0	0.333
Mint x	0	0	0	0	0.25	0	0
Mustard x	0	0	0	0	0	0	0
plant x	0	0	0	0	0	0	0
<i>Plantago major</i>	0	0	0	0	0	0	0
<i>Poa palustris</i>	0.5	0.5	0.25	0.333	0.25	0.333	0.333
<i>Poa trivialis</i>	0	0	0	0	0	0	0
<i>Polygonum amphibium</i>	0	0	0.25	0	0	0	0
<i>Polygonum lapathifolium</i>	0	0	0	0	0	0	0
<i>Potentilla norvegica</i>	0.5	0	0.25	0	0.25	0.333	0.667
<i>Ranunculus sceleratus</i>	0	0.25	0.5	0	0	0.333	0.333
<i>Rorripa islandica</i>	0.25	0.25	0.75	0	0	0.333	0.333
<i>Rumex maritimus</i>	0.5	0.5	0.75	0.333	0	0	0
<i>Scutellaria galericulata</i>	0	0	0	0	0	0	0
<i>Setaria vividis</i>	0	0	0	0	0	0	0
<i>Sium suave</i>	0	0	0	0	0	0.333	0
<i>Solidago canadensis var c</i>	0	0	0	0	0	0	0
<i>Sonchus arvensis</i>	0	0	0	0.333	0	0	0
<i>Stachys palustris</i>	0	0	0	0	0	0	0
<i>Stellaria crassifolia</i>	0	0	0	0	0	0	0
Stink	0	0	0	0	0	0	0
<i>Taraxacum officinale</i>	0	0	0	0	0	0	0
<i>Thlaspi arvense</i>	0	0	0	0	0	0	0
<i>Typha latifolia</i>	0	0	0	0	0	0	0
<i>Urtica dioica</i>	0.25	0	0	1	0.75	1	0.667
<i>Vicia americana</i>	0	0	0	0	0	0	0
Species e	0	0	0	0	0	0	0
Species f	0	0	0	0	0	0	0
Species q	0	0	0	0	0	0	0

Appendix 2.6 Average % cover values for each transect

Meadow	1	1	1	1	1	2
Transect	1	2	3	4	5	1
Species						
<i>Calamagrostis neglecta</i>	26.67	43.33	54.50	50.71	54.00	14.44
<i>Carex atherodes</i>	2.78	7.22	10.00	16.43	26.00	35.00
<i>Cirsium arvense</i>	18.89	6.67	1.00	1.43	4.00	27.78
<i>Solidago canadensis</i>	2.22	4.44	0.00	0.00	0.00	2.78
<i>Sonchus arvensis</i>	21.67	12.78	4.00	2.14	2.00	17.78
<i>Urtica dioica</i>	1.11	0.00	0.50	0.00	0.00	20.56
<i>Mentha arvensis</i>	0.00	1.11	0.00	1.43	0.00	1.11
<i>Polygonum amphibium</i>	0.00	0.00	0.00	2.86	2.00	0.00
<i>Achillea millefolium</i>	1.11	0.00	0.00	0.00	0.00	0.00
<i>Acorus calamus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agropyron trachycaulum</i>	1.11	0.00	0.00	0.00	0.00	0.00
<i>Agrostis scabra</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Anemone canadensis</i>	1.67	3.89	8.00	2.86	0.00	0.00
<i>Aster junciformis</i>	14.44	5.56	5.00	0.00	5.00	8.89
<i>Aster laevis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Beckmannia syzigachne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Bidens cernua</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Bromus ciliatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex aquatilis</i>	0.00	0.00	12.50	2.14	0.00	0.00
<i>Carex caespitosus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex rostrata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cicuta bulbifera</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epilobium glandulosum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Equisetum variegatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Erysimum inconspicuum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fragaria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galeopsis tetrahit</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galium trifidum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Geum aleppicum</i>	0.00	0.00	0.00	0.00	2.00	0.00
<i>Glyceria grandis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria striata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Impatiens biflora</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Juncus balticus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lemna minor</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus asper</i>	0.00	2.78	0.50	0.00	0.00	0.00
<i>Lycopus uniflorus</i>	0.00	1.11	0.50	1.43	0.00	0.00
<i>Parnassia palustris</i>	0.00	2.22	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites sagittatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites</i> sp.	0.00	0.00	0.00	0.00	0.00	2.78

Appendix 2.6

Meadow	1	1	1	1	1	2
Transect	1	2	3	4	5	1
Species						
Phalaris arundinacea	0.00	0.56	1.50	0.00	6.00	0.00
Phleum pratense	0.00	0.00	0.00	0.00	0.00	0.00
plant x	0.00	0.00	0.00	0.00	0.00	0.00
Plantago major	0.00	0.00	0.00	0.00	0.00	0.00
Poa palustris	10.00	2.78	0.00	3.57	0.00	0.00
Polygonum lapathifolium	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla anserina	0.00	0.56	0.00	0.00	0.00	0.00
Potentilla norvegica	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus sceleratus	0.00	0.00	0.00	0.00	0.00	0.00
Ribes oxyacanthoides	0.00	0.00	0.00	0.00	0.00	0.00
Rorripa islandica	0.00	0.00	0.00	0.00	0.00	0.00
Rubus strigosus	0.00	0.00	0.00	0.00	0.00	0.00
Rudbeckia serotina	0.00	1.11	0.00	0.00	0.00	0.00
Rumex maritimus	0.00	0.00	0.00	0.00	0.00	0.00
Sagittaria cuneata	0.00	0.00	0.00	0.00	0.00	0.00
Salix sp A	0.00	0.00	0.00	0.00	0.00	0.00
Salix sp B	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus caespitosus	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus microcarpus	0.00	1.67	0.00	0.00	0.00	0.00
Scirpus validus	0.00	0.00	0.00	0.00	0.00	0.00
Scutellaria lateriflora	0.00	0.00	0.00	0.00	0.00	0.00
Sium suave	0.00	0.00	0.00	0.00	0.00	0.00
Sparganium eurycarpum	0.00	0.00	0.00	0.00	0.00	0.00
Stachys palustris	0.00	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia	0.00	0.00	0.00	0.00	0.00	0.00
Vicia americana	0.56	0.00	0.00	0.00	0.00	0.00
Viola sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	2	2	2	2	3	3
Transect	2	3	4	5	1	2
Species						
<i>Calamagrostis neglecta</i>	0.00	2.00	0.00	8.33	32.86	27.14
<i>Carex atherodes</i>	64.44	48.00	72.78	67.22	40.00	34.29
<i>Cirsium arvense</i>	17.78	7.00	5.56	4.44	13.57	2.86
<i>Solidago canadensis</i>	0.00	0.00	0.00	0.00	0.00	1.43
<i>Sonchus arvensis</i>	0.00	0.00	0.00	2.22	7.14	1.43
<i>Urtica dioica</i>	1.11	11.50	2.78	7.78	22.14	4.29
<i>Mentha arvensis</i>	6.67	6.50	4.44	8.89	5.71	10.71
<i>Polygonum amphibium</i>	4.44	0.00	0.00	0.00	2.86	4.29
<i>Achillea millefolium</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Acorus calamus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agropyron trachycaulum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agrostis scabra</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Anemone canadensis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Aster junciformis</i>	1.11	0.00	0.00	0.00	0.00	2.86
<i>Aster laevis</i>	0.00	2.00	0.00	0.00	0.00	0.00
<i>Beckmannia syzigachne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Bidens cernua</i>	0.00	0.00	0.00	0.00	0.00	5.00
<i>Bromus ciliatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex aquatilis</i>	4.44	0.00	0.00	0.00	0.00	1.43
<i>Carex caespitosus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex rostrata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cicuta bulbifera</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epilobium glandulosum</i>	0.00	0.00	0.00	0.00	0.00	2.14
<i>Equisetum variegatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Erysimum inconspicuum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fragaria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galeopsis tetrahit</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galium trifidum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Geum aleppicum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria grandis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria striata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Impatiens biflora</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Juncus balticus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lemna minor</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus asper</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus uniflorus</i>	4.44	1.00	0.00	0.00	0.00	2.86
<i>Parnassia palustris</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites sagittatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites</i> sp.	4.44	0.00	0.00	2.78	0.00	0.00

Appendix 2.6

Meadow	2	2	2	2	3	3
Transect	2	3	4	5	1	2
Species						
Phalaris arundinacea	0.00	3.00	0.00	0.00	0.00	0.00
Phleum pratense	0.00	0.00	0.00	0.00	0.00	0.00
plant x	0.00	0.00	0.00	0.00	0.00	0.00
Plantago major	0.00	0.00	0.00	0.00	0.00	0.00
Poa palustris	0.00	0.00	0.00	0.00	0.00	0.00
Polygonum lapathifolium	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla anserina	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla norvegica	2.22	0.00	0.00	0.00	0.00	2.86
Ranunculus sceleratus	0.00	0.00	0.00	0.00	0.00	0.00
Ribes oxyacanthoides	0.00	0.00	0.00	0.00	0.00	0.00
Rorripa islandica	0.00	0.00	0.00	0.00	0.00	0.00
Rubus strigosus	0.00	0.00	0.00	0.00	0.00	0.00
Rudbeckia serotina	0.00	0.00	0.00	0.00	0.00	0.00
Rumex maritimus	0.00	0.00	0.00	0.00	0.00	1.43
Sagittaria cuneata	0.00	0.00	0.00	0.00	0.00	0.71
Salix sp A	0.00	0.00	0.00	0.00	0.00	0.00
Salix sp B	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus caespitosus	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus microcarpus	0.00	1.00	2.22	0.00	0.00	0.00
Scirpus validus	0.00	0.00	0.00	0.00	0.00	0.00
Scutellaria lateriflora	0.00	0.00	0.00	0.00	0.00	0.00
Sium suave	0.00	0.00	0.00	0.00	0.00	0.00
Sparganium eurycarpum	0.00	0.00	0.00	0.00	0.00	0.00
Stachys palustris	0.00	0.00	0.00	0.00	5.71	1.43
Taraxacum officinale	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia	0.00	0.00	0.00	1.11	0.00	0.00
Vicia americana	0.00	0.00	0.00	0.00	0.00	0.00
Viola sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	3	3	5	5	5	5
Transect	3	4	1	2	3	4
Species						
<i>Calamagrostis neglecta</i>	25.00	72.50	22.14	24.29	13.00	24.00
<i>Carex atherodes</i>	42.50	7.50	7.14	40.00	54.00	31.00
<i>Cirsium arvense</i>	0.00	0.00	9.29	10.71	4.00	14.00
<i>Solidago canadensis</i>	0.00	0.00	4.29	0.00	0.00	6.00
<i>Sonchus arvensis</i>	0.00	0.00	11.43	1.43	7.00	0.00
<i>Urtica dioica</i>	5.00	0.00	15.00	7.14	4.00	1.00
<i>Mentha arvensis</i>	0.00	0.00	0.00	9.29	6.00	2.00
<i>Polygonum amphibium</i>	0.00	0.00	4.29	4.29	6.00	4.00
<i>Achillea millefolium</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Acorus calamus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agropyron trachycaulum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agrostis scabra</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Anemone canadensis</i>	0.00	0.00	5.71	0.00	7.00	8.00
<i>Aster junciformis</i>	0.00	0.00	7.14	0.00	4.00	4.00
<i>Aster laevis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Beckmannia syzigachne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Bidens cernua</i>	12.50	0.00	0.00	0.00	0.00	0.00
<i>Bromus ciliatus</i>	0.00	0.00	2.86	0.00	0.00	0.00
<i>Carex aquatilis</i>	0.00	7.50	0.00	0.00	0.00	0.00
<i>Carex caespitosus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex rostrata</i>	0.00	0.00	0.00	10.00	0.00	0.00
<i>Cicuta bulbifera</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epilobium glandulosum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Equisetum variegatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Erysimum inconspicuum</i>	0.00	0.00	8.57	0.00	0.00	0.00
<i>Fragaria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galeopsis tetrahit</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galium trifidum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Geum aleppicum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria grandis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria striata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i>	0.00	0.00	0.00	2.86	0.00	0.00
<i>Impatiens biflora</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Juncus balticus</i>	0.00	0.00	0.00	0.00	0.00	4.00
<i>Lemna minor</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus asper</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus uniflorus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Parnassia palustris</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites sagittatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	3	3	5	5	5	5
Transect	3	4	1	2	3	4
Species						
Phalaris arundinacea	0.00	0.00	0.00	0.00	0.00	10.00
Phleum pratense	0.00	0.00	0.00	0.00	0.00	0.00
plant x	0.00	0.00	0.00	0.00	0.00	0.00
Plantago major	0.00	0.00	0.00	0.00	0.00	0.00
Poa palustris	0.00	0.00	0.00	0.00	0.00	0.00
Polygonum lapathifolium	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla anserina	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla norvegica	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus sceleratus	0.00	0.00	0.00	0.00	0.00	0.00
Ribes oxyacanthoides	0.00	0.00	4.29	0.00	0.00	0.00
Rorripa islandica	0.00	0.00	0.00	0.00	0.00	0.00
Rubus strigosus	0.00	0.00	26.43	0.00	0.00	0.00
Rudbeckia serotina	0.00	0.00	0.00	0.00	0.00	0.00
Rumex maritimus	0.00	0.00	0.00	0.00	0.00	0.00
Sagittaria cuneata	0.00	0.00	0.00	0.00	0.00	0.00
Salix sp A	0.00	0.00	0.00	0.00	0.00	0.00
Salix sp B	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus caespitosus	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus microcarpus	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus validus	0.00	0.00	0.00	0.00	0.00	0.00
Scutellaria lateriflora	0.00	0.00	0.00	0.00	0.00	0.00
Sium suave	0.00	5.00	0.00	0.00	0.00	0.00
Sparganium eurycarpum	10.00	0.00	0.00	0.00	0.00	0.00
Stachys palustris	0.00	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia	0.00	0.00	0.00	0.00	0.00	0.00
Vicia americana	0.00	0.00	0.00	0.00	0.00	0.00
Viola sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	7	7	7	7	8	8
Transect	1	2	3	4	1	2
Species						
<i>Calamagrostis neglecta</i>	57.14	17.14	40.00	61.43	31.00	12.50
<i>Carex atherodes</i>	8.57	7.14	5.00	18.57	35.67	12.50
<i>Cirsium arvense</i>	29.29	10.71	6.67	0.00	12.67	0.00
<i>Solidago canadensis</i>	0.00	0.00	0.00	0.00	4.33	0.00
<i>Sonchus arvensis</i>	1.43	0.00	1.67	1.43	0.00	0.42
<i>Urtica dioica</i>	12.86	8.57	5.83	1.43	4.67	0.83
<i>Mentha arvensis</i>	0.00	5.71	7.50	5.00	0.33	0.83
<i>Polygonum amphibium</i>	0.00	12.86	1.67	1.43	0.00	15.42
<i>Achillea millefolium</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Acorus calamus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agropyron trachycaulum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agrostis scabra</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Anemone canadensis</i>	0.00	0.00	0.00	0.00	6.67	0.00
<i>Aster junciformis</i>	0.00	0.00	4.17	0.00	6.00	0.00
<i>Aster laevis</i>	0.00	0.00	0.00	0.00	1.33	0.00
<i>Beckmannia syzigachne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Bidens cernua</i>	0.00	25.00	12.50	0.00	0.00	0.00
<i>Bromus ciliatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex aquatilis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex caespitosus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex rostrata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cicuta bulbifera</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epilobium glandulosum</i>	0.00	3.57	0.00	0.00	0.33	0.00
<i>Equisetum variegatum</i>	0.00	0.00	1.67	0.00	0.00	0.00
<i>Erysimum inconspicuum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fragaria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galeopsis tetrahit</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galium trifidum</i>	0.00	24.29	0.00	1.43	0.00	10.42
<i>Geum aleppicum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria grandis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria striata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Impatiens biflora</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Juncus balticus</i>	0.00	0.00	3.33	0.00	0.00	0.00
<i>Lemna minor</i>	0.00	4.29	0.00	0.00	0.00	0.00
<i>Lycopus asper</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus uniflorus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Parnassia palustris</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i>	1.43	0.00	1.67	2.86	0.00	0.00
<i>Petasites sagittatus</i>	3.57	2.86	0.00	2.86	0.00	0.00
<i>Petasites</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow Transect Species	7 1	7 2	7 3	7 4	8 1	8 2
Phalaris arundinacea	0.00	0.00	0.00	0.00	0.00	0.00
Phleum pratense	0.00	0.00	0.00	0.00	0.00	0.00
plant x	0.00	0.00	0.00	0.00	0.00	0.00
Plantago major	0.00	0.00	0.00	0.00	0.00	0.00
Poa palustris	0.00	1.43	0.00	0.00	0.00	0.00
Polygonum lapathifolium	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla anserina	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla norvegica	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus sceleratus	0.00	0.00	0.00	0.00	0.00	0.00
Ribes oxyacanthoides	0.00	0.00	0.00	0.00	0.00	0.00
Rorripa islandica	0.00	0.00	3.33	0.00	0.00	0.00
Rubus strigosus	4.29	0.00	1.67	0.00	0.00	0.00
Rudbeckia serotina	0.00	0.00	0.00	0.00	0.00	0.00
Rumex maritimus	0.00	1.43	4.17	0.00	0.00	0.00
Sagittaria cuneata	0.00	0.00	0.00	0.00	0.00	1.25
Salix sp A	0.00	0.00	5.00	0.00	0.00	0.00
Salix sp B	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus caespitosus	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus microcarpus	0.00	0.00	0.00	0.00	1.33	0.00
Scirpus validus	0.00	0.00	0.00	0.00	0.00	0.00
Scutellaria lateriflora	0.00	0.00	0.00	0.00	0.00	0.00
Sium suave	0.00	0.00	0.00	0.00	0.00	1.25
Sparganium eurycarpum	0.00	4.29	1.67	0.00	0.00	0.00
Stachys palustris	0.00	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia	0.00	0.00	0.00	0.00	0.00	0.00
Vicia americana	0.00	0.00	0.00	0.00	0.00	0.00
Viola sp.	0.00	0.00	1.67	0.00	0.00	0.00

Appendix 2.6

Meadow	8	8	8	11	11	11
Transect	3	4	5	1	2	3
Species						
<i>Calamagrostis neglecta</i>	28.89	50.00	70.00	12.86	1.82	8.75
<i>Carex atherodes</i>	3.33	30.00	7.14	51.43	30.45	31.88
<i>Cirsium arvense</i>	0.00	0.00	0.00	15.00	1.36	16.88
<i>Solidago canadensis</i>	5.56	0.00	0.00	2.86	0.00	3.13
<i>Sonchus arvensis</i>	0.00	0.00	0.00	19.29	0.91	7.50
<i>Urtica dioica</i>	0.00	0.00	0.00	5.00	0.91	1.25
<i>Mentha arvensis</i>	0.00	0.00	0.00	1.43	2.27	3.75
<i>Polygonum amphibium</i>	5.56	2.50	5.00	0.00	5.00	1.25
<i>Achillea millefolium</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Acorus calamus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agropyron trachycaulum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agrostis scabra</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Anemone canadensis</i>	7.78	0.00	0.00	1.43	0.00	2.50
<i>Aster junciformis</i>	0.00	0.00	0.00	13.57	6.36	6.25
<i>Aster laevis</i>	1.11	0.00	0.00	0.00	0.00	0.00
<i>Beckmannia syzigachne</i>	0.00	0.00	0.00	0.00	0.91	0.00
<i>Bidens cernua</i>	0.00	0.00	0.00	0.00	15.00	3.13
<i>Bromus ciliatus</i>	3.33	0.00	0.00	0.00	0.00	3.75
<i>Carex aquatilis</i>	0.00	0.00	0.00	0.00	2.73	0.00
<i>Carex caespitosus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex rostrata</i>	2.22	3.75	4.29	0.00	0.00	0.00
<i>Cicuta bulbifera</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epilobium glandulosum</i>	0.00	0.00	0.00	0.00	2.73	0.00
<i>Equisetum variegatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Erysimum inconspicuum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fragaria</i> sp.	0.00	0.00	0.00	0.00	3.64	0.00
<i>Galeopsis tetrahit</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galium trifidum</i>	0.56	0.00	0.00	0.00	15.00	4.38
<i>Geum aleppicum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria grandis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria striata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Impatiens biflora</i>	0.00	0.00	0.00	0.00	1.36	0.00
<i>Juncus balticus</i>	0.56	0.00	0.00	0.00	0.00	0.00
<i>Lemna minor</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus asper</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus uniflorus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Parnassia palustris</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites sagittatus</i>	0.00	0.00	0.00	0.00	0.00	1.25
<i>Petasites</i> sp.	1.11	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	8	8	8	11	11	11
Transect	3	4	5	1	2	3
Species						
Phalaris arundinacea	0.00	0.00	0.00	0.00	2.27	1.25
Phleum pratense	0.00	0.00	0.00	0.00	3.64	0.00
plant x	0.00	0.00	0.00	0.00	0.00	0.00
Plantago major	0.00	0.00	0.00	0.00	0.00	0.00
Poa palustris	0.00	0.00	0.00	12.86	10.00	2.50
Polygonum lapathifolium	0.00	0.00	0.00	1.43	0.00	0.00
Potentilla anserina	0.00	0.00	0.00	1.43	0.00	0.00
Potentilla norvegica	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus sceleratus	0.00	0.00	0.00	0.00	1.36	0.00
Ribes oxyacanthoides	0.00	0.00	0.00	0.00	0.00	0.00
Rorripa islandica	0.00	0.00	0.00	0.00	3.64	0.63
Rubus strigosus	0.00	0.00	0.00	0.00	0.00	0.00
Rudbeckia serotina	0.00	0.00	0.00	0.00	0.00	0.00
Rumex maritimus	0.00	0.00	0.00	0.00	6.36	1.88
Sagittaria cuneata	2.22	0.00	0.00	0.00	0.00	0.00
Salix sp A	0.00	3.75	0.00	0.00	0.00	0.00
Salix sp B	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus caespitosus	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus microcarpus	2.22	1.25	0.00	0.00	5.91	0.00
Scirpus validus	0.00	0.00	0.00	0.00	0.00	0.00
Scutellaria lateriflora	0.00	0.00	0.00	0.00	0.00	0.00
Sium suave	0.00	0.00	0.00	0.00	0.91	0.00
Sparganium eurycarpum	0.00	0.00	0.00	0.00	0.00	0.00
Stachys palustris	0.00	0.00	0.00	5.00	2.27	15.00
Taraxacum officinale	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia	0.00	0.00	0.00	0.00	0.00	0.00
Vicia americana	0.00	0.00	0.00	0.00	0.00	0.00
Viola sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	11	12	12	12	12	14
Transect	4	1	2	3	4	1
Species						
<i>Calamagrostis neglecta</i>	13.33	25.00	6.88	2.50	28.00	2.86
<i>Carex atherodes</i>	45.83	43.75	26.88	28.75	35.00	42.86
<i>Cirsium arvense</i>	5.00	15.63	0.00	2.50	4.00	10.71
<i>Solidago canadensis</i>	2.50	0.00	0.00	0.00	2.00	0.00
<i>Sonchus arvensis</i>	0.00	5.00	1.25	17.50	4.00	12.14
<i>Urtica dioica</i>	5.00	0.63	0.00	0.00	2.00	16.43
<i>Mentha arvensis</i>	7.50	5.00	1.88	8.75	1.00	2.86
<i>Polygonum amphibium</i>	9.17	3.75	5.00	5.00	8.00	0.00
<i>Achillea millefolium</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Acorus calamus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agropyron trachycaulum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agrostis scabra</i>	0.00	0.00	13.75	0.00	0.00	0.00
<i>Anemone canadensis</i>	0.00	0.00	0.00	0.00	0.00	5.71
<i>Aster junciformis</i>	7.50	8.75	1.88	0.00	0.00	8.57
<i>Aster laevis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Beckmannia syzigachne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Bidens cernua</i>	0.00	0.00	0.00	0.00	1.00	0.00
<i>Bromus ciliatus</i>	0.00	0.00	0.00	0.00	4.00	2.86
<i>Carex aquatilis</i>	6.67	0.00	6.25	27.50	0.00	0.00
<i>Carex caespitosus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex rostrata</i>	0.00	0.00	0.00	22.50	4.00	1.43
<i>Cicuta bulbifera</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epilobium glandulosum</i>	0.00	0.00	0.00	0.00	1.00	0.00
<i>Equisetum variegatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Erysimum inconspicuum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fragaria</i> sp.	0.00	0.00	0.00	0.00	0.00	1.43
<i>Galeopsis tetrahit</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galium trifidum</i>	0.00	0.00	0.00	0.00	2.00	0.00
<i>Geum aleppicum</i>	0.00	0.00	0.00	2.50	1.00	0.00
<i>Glyceria grandis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Glyceria striata</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Impatiens biflora</i>	5.00	2.50	1.25	0.00	0.00	1.43
<i>Juncus balticus</i>	0.00	0.00	1.88	0.00	0.00	0.00
<i>Lemna minor</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus asper</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus uniflorus</i>	0.00	0.00	0.00	0.00	0.00	7.14
<i>Parnassia palustris</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites sagittatus</i>	0.00	0.00	0.00	0.00	0.00	1.43
<i>Petasites</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	11	12	12	12	12	14
Transect	4	1	2	3	4	1
Species						
Phalaris arundinacea	7.50	0.00	3.13	5.00	0.00	0.00
Phleum pratense	0.00	0.00	0.00	0.00	0.00	0.00
plant x	0.00	0.00	0.00	0.00	0.00	0.00
Plantago major	0.00	0.00	0.00	0.00	0.00	0.00
Poa palustris	1.67	0.00	0.00	2.50	0.00	1.43
Polygonum lapathifolium	0.00	0.00	0.00	2.50	0.00	0.00
Potentilla anserina	0.00	0.00	0.00	0.00	0.00	2.86
Potentilla norvegica	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus sceleratus	0.00	0.00	0.00	0.00	0.00	0.00
Ribes oxyacanthoides	0.00	0.00	0.00	0.00	0.00	0.00
Rorripa islandica	0.00	0.00	0.00	0.00	0.00	0.00
Rubus strigosus	0.00	4.38	0.00	0.00	0.00	0.00
Rudbeckia serotina	0.00	0.00	0.00	0.00	0.00	0.00
Rumex maritimus	0.00	0.00	0.00	0.00	0.00	0.00
Sagittaria cuneata	0.00	0.00	0.00	0.00	0.00	0.00
Salix sp A	0.00	0.00	0.00	0.00	6.00	0.00
Salix sp B	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus caespitosus	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus microcarpus	0.00	0.00	1.88	0.00	0.00	0.00
Scirpus validus	0.00	0.00	0.00	0.00	0.00	0.00
Scutellaria lateriflora	0.00	0.00	0.00	0.00	0.00	0.00
Sium suave	0.00	0.00	0.00	0.00	0.00	0.00
Sparganium eurycarpum	0.00	0.00	6.25	0.00	0.00	0.00
Stachys palustris	8.33	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia	0.00	0.00	0.00	0.00	1.00	0.00
Vicia americana	0.00	1.25	2.50	0.00	0.00	2.86
Viola sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	14	14	14	15	15	15
Transect	2	3	4	1	2	3
Species						
<i>Calamagrostis neglecta</i>	17.14	0.00	0.00	7.50	4.50	17.50
<i>Carex atherodes</i>	5.71	28.33	21.67	36.50	32.00	54.50
<i>Cirsium arvense</i>	7.14	4.17	3.33	34.00	30.00	12.00
<i>Solidago canadensis</i>	0.00	0.00	0.00	4.50	2.00	1.00
<i>Sonchus arvensis</i>	2.14	0.00	0.00	22.00	8.50	3.00
<i>Urtica dioica</i>	0.00	0.00	5.00	0.00	0.00	5.00
<i>Mentha arvensis</i>	4.29	21.67	16.67	5.50	11.00	7.00
<i>Polygonum amphibium</i>	6.43	1.67	4.17	0.00	0.00	0.00
<i>Achillea millefolium</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Acorus calamus</i>	0.00	5.00	0.00	0.00	0.00	0.00
<i>Agropyron trachycaulum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Agrostis scabra</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Anemone canadensis</i>	0.00	0.00	0.00	0.00	4.00	2.50
<i>Aster junciformis</i>	7.86	0.00	0.00	2.00	9.00	2.00
<i>Aster laevis</i>	0.00	0.00	0.00	0.00	2.50	2.50
<i>Beckmannia syzigachne</i>	2.86	0.00	0.00	0.00	2.50	0.00
<i>Bidens cernua</i>	23.57	1.67	0.00	0.00	0.00	0.00
<i>Bromus ciliatus</i>	0.00	0.00	1.67	4.50	0.00	2.50
<i>Carex aquatilis</i>	0.00	0.00	15.83	0.00	0.00	0.00
<i>Carex caespitosus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex rostrata</i>	0.00	13.33	0.00	0.00	0.00	0.00
<i>Cicuta bulbifera</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epilobium glandulosum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Equisetum variegatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Erysimum inconspicuum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fragaria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galeopsis tetrahit</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Galium trifidum</i>	2.86	3.33	0.00	0.00	0.00	0.00
<i>Geum aleppicum</i>	0.00	0.00	0.00	1.50	1.50	0.00
<i>Glyceria grandis</i>	0.00	0.00	0.00	0.00	17.00	0.00
<i>Glyceria striata</i>	1.43	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i>	1.43	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Impatiens biflora</i>	0.00	0.00	1.67	0.00	2.00	0.00
<i>Juncus balticus</i>	2.86	3.33	0.00	0.00	0.00	0.00
<i>Lemna minor</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus asper</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopus uniflorus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Parnassia palustris</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Petasites sagittatus</i>	0.00	0.00	0.00	0.00	0.00	3.00
<i>Petasites</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	14	14	14	15	15	15
Transect	2	3	4	1	2	3
Species						
<i>Phalaris arundinacea</i>	0.00	0.00	0.00	3.50	3.50	2.50
<i>Phleum pratense</i>	0.00	0.00	0.00	0.00	0.00	0.00
plant x	0.00	0.00	0.00	0.00	0.00	0.00
<i>Plantago major</i>	0.00	0.00	0.00	2.50	0.00	0.00
<i>Poa palustris</i>	2.14	0.00	0.00	7.50	1.50	2.00
<i>Polygonum lapathifolium</i>	0.71	0.00	0.00	0.00	0.00	0.00
<i>Potentilla anserina</i>	0.71	3.33	1.67	4.00	0.00	0.00
<i>Potentilla norvegica</i>	0.00	3.33	0.00	0.00	0.00	0.50
<i>Ranunculus sceleratus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ribes oxyacanthoides</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Rorripa islandica</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Rubus strigosus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Rudbeckia serotina</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Rumex maritimus</i>	4.29	0.00	0.00	0.00	0.00	0.00
<i>Sagittaria cuneata</i>	3.57	1.67	0.00	0.00	0.00	0.00
<i>Salix</i> sp A	3.57	0.00	0.00	0.00	0.00	0.00
<i>Salix</i> sp B	0.00	0.00	0.00	0.00	0.00	3.00
<i>Scirpus caespitosus</i>	18.57	15.83	0.00	0.00	0.00	0.00
<i>Scirpus microcarpus</i>	0.00	0.00	0.00	0.00	4.00	0.00
<i>Scirpus validus</i>	0.71	0.00	0.00	0.00	0.00	0.00
<i>Scutellaria lateriflora</i>	0.00	0.00	4.17	0.00	0.00	0.00
<i>Sium suave</i>	1.43	0.00	0.00	0.00	2.00	0.00
<i>Sparganium eurycarpum</i>	11.43	0.00	0.00	0.00	0.00	0.00
<i>Stachys palustris</i>	0.00	0.00	0.00	3.00	0.00	0.00
<i>Taraxacum officinale</i>	0.00	0.00	0.00	0.00	0.50	0.00
<i>Typha latifolia</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Vicia americana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Viola</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow	15	p4	p4	p4	p4
Transect	4	1	2	3	4
Species					
<i>Calamagrostis neglecta</i>	14.00	50.00	4.44	8.00	23.75
<i>Carex atherodes</i>	52.00	16.43	0.00	40.00	12.50
<i>Cirsium arvense</i>	10.50	4.29	17.22	12.00	16.25
<i>Solidago canadensis</i>	3.00	0.00	0.00	0.00	0.00
<i>Sonchus arvensis</i>	0.00	0.00	0.00	0.00	0.00
<i>Urtica dioica</i>	6.50	11.43	11.11	3.00	12.50
<i>Mentha arvensis</i>	7.00	14.29	15.56	1.00	3.75
<i>Polygonum amphibium</i>	0.00	1.43	1.11	0.00	7.50
<i>Achillea millefolium</i>	0.00	0.00	0.00	0.00	0.00
<i>Acorus calamus</i>	0.00	0.00	0.00	0.00	0.00
<i>Agropyron trachycaulum</i>	0.00	0.00	0.00	0.00	0.00
<i>Agrostis scabra</i>	0.00	0.00	0.00	0.00	0.00
<i>Anemone canadensis</i>	0.00	0.00	0.00	0.00	0.00
<i>Aster junciformis</i>	4.00	0.00	0.00	0.00	0.00
<i>Aster laevis</i>	0.00	0.00	0.00	0.00	0.00
<i>Beckmannia syzigachne</i>	0.00	0.00	0.00	0.00	0.00
<i>Bidens cernua</i>	0.00	1.43	46.67	0.00	6.25
<i>Bromus ciliatus</i>	0.00	0.00	0.00	0.00	0.00
<i>Carex aquatilis</i>	0.00	0.00	0.00	0.00	0.00
<i>Carex caespitosus</i>	0.00	0.00	0.00	0.00	0.00
<i>Carex rostrata</i>	0.00	0.00	0.00	0.00	0.00
<i>Cicuta bulbifera</i>	0.00	0.00	1.11	0.00	0.00
<i>Epilobium glandulosum</i>	0.00	0.00	4.44	0.00	0.00
<i>Equisetum variegatum</i>	0.00	0.00	0.00	0.00	0.00
<i>Erysimum inconspicuum</i>	0.00	0.00	0.00	0.00	0.00
<i>Fragaria</i> sp.	0.00	0.00	8.33	0.00	1.25
<i>Galeopsis tetrahit</i>	0.00	0.00	8.33	8.00	0.00
<i>Galium trifidum</i>	0.00	0.00	18.89	10.00	5.00
<i>Geum aleppicum</i>	0.00	0.00	0.00	0.00	0.00
<i>Glyceria grandis</i>	0.00	0.00	0.00	0.00	0.00
<i>Glyceria striata</i>	0.00	0.00	0.00	0.00	0.00
<i>Habenaria hyperborea</i>	0.00	0.00	0.00	0.00	0.00
<i>Heracleum lanatum</i>	0.00	0.00	0.00	0.00	0.00
<i>Impatiens biflora</i>	0.00	2.14	0.00	0.00	0.00
<i>Juncus balticus</i>	0.00	0.00	0.00	0.00	0.00
<i>Lemna minor</i>	0.00	0.00	3.33	0.00	5.00
<i>Lycopus asper</i>	0.00	0.00	0.00	0.00	0.00
<i>Lycopus uniflorus</i>	0.00	1.43	3.33	0.00	0.00
<i>Parnassia palustris</i>	0.00	0.00	0.00	0.00	0.00
<i>Petasites palmatus</i>	0.00	0.00	0.00	0.00	0.00
<i>Petasites sagittatus</i>	0.00	1.43	0.00	0.00	0.00
<i>Petasites</i> sp.	0.00	0.00	0.00	0.00	0.00

Appendix 2.6

Meadow Transect Species	15 4	p4 1	p4 2	p4 3	p4 4
Phalaris arundinacea	0.00	0.00	0.00	0.00	0.00
Phleum pratense	0.00	0.00	0.00	0.00	0.00
plant x	0.00	0.00	1.11	0.00	0.00
Plantago major	0.00	0.00	0.00	0.00	0.00
Poa palustris	0.00	1.43	4.44	0.00	0.00
Polygonum lapathifolium	0.00	1.43	6.67	0.00	0.00
Potentilla anserina	0.00	0.00	0.00	0.00	0.00
Potentilla norvegica	0.00	0.00	3.89	0.00	0.00
Ranunculus sceleratus	0.00	0.00	3.33	0.00	0.00
Ribes oxyacanthoides	0.00	0.00	0.00	0.00	0.00
Rorripa islandica	0.00	0.00	1.11	1.00	0.00
Rubus strigosus	0.00	0.00	0.00	0.00	0.00
Rudbeckia serotina	0.00	0.00	0.00	0.00	0.00
Rumex maritimus	0.00	0.00	2.22	0.00	0.00
Sagittaria cuneata	0.00	0.00	0.00	0.00	0.00
Salix sp A	0.00	0.00	0.00	0.00	0.00
Salix sp B	0.00	0.00	0.00	0.00	0.00
Scirpus caespitosus	0.00	0.00	0.00	0.00	0.00
Scirpus microcarpus	0.00	0.00	0.00	0.00	0.00
Scirpus validus	0.00	0.00	0.00	0.00	0.00
Scutellaria lateriflora	0.00	0.00	0.00	0.00	0.00
Sium suave	0.00	0.00	5.56	0.00	7.50
Sparganium eurycarpum	0.00	0.00	0.00	4.00	0.00
Stachys palustris	0.00	0.00	2.22	0.00	0.00
Taraxacum officinale	0.00	0.00	0.00	0.00	0.00
Typha latifolia	0.00	0.00	1.11	0.00	0.00
Vicia americana	0.00	0.71	0.00	0.00	0.00
Viola sp.	0.00	0.00	0.00	0.00	0.00

Appendix 2.7 Authorities

Species	Authority	Species	Authority
<i>Achillea millefolium</i>	L.	<i>Lycopus asper</i>	Greene
<i>Acorus calamus</i>	L.	<i>Lycopus uniflorus</i>	Michx.
<i>Agropyron trachycaulum</i>	(L.) Gaertn.	<i>Medicago lupulina</i>	L.
<i>Agrostis scabra</i>	Willd.	<i>Mentha arvensis</i>	L.
<i>Alnus rugosa</i>	(Du Roi) Clausen	<i>Parnassia palustris</i>	L.
<i>Alopecurus aequalis</i>	Sobol.	<i>Petasites palmatus</i>	(Ait.) A. Gray
<i>Amaranthus retroflexus</i>	L.	<i>Petasites sagittatus</i>	(Pursh) A. Gray
<i>Anemone canadensis</i>	L.	<i>Phalaris arundinacea</i>	L.
<i>Aster junciformis</i>	Rydb.	<i>Phleum pratense</i>	L.
<i>Aster laevis</i>	L.	<i>Picae glauca</i>	(Moench) Voss
<i>Aster simplex</i>	Willd.	<i>Plantago major</i>	L.
<i>Beckmannia syzigachne</i>	(Steud.) Fern.	<i>Poa palustris</i>	L.
<i>Bidens cernua</i>	L.	<i>Poa trivialis</i>	L.
<i>Bromus ciliatus</i>	L.	<i>Polygonum amphibium</i>	L.
<i>Bromus inermis</i>	Leyss.	<i>Polygonum lapathifolium</i>	L.
<i>Calamagrostis canadensis</i>	(Michx.) Beauv.	<i>Potentilla anserina</i>	L.
<i>Calamagrostis neglecta</i>	(Ehrh.) Gaertn.	<i>Potentilla norvegica</i>	L.
<i>Carex aquatilis</i>	Wahl.	<i>Ranunculus aquatilis</i>	L.
<i>Carex atherodes</i>	Spreng.	<i>Ranunculus sceleratus</i>	L.
<i>Carex rostrata</i>	Stokes	<i>Ribes oxyacanthoides</i>	L.
<i>Carex sychrocephala</i>	Carey	<i>Rorippa islandica</i>	(Oeder) Borbas
<i>Chenopodium album</i>	L.	<i>Rubus strigosus</i>	Michx.
<i>Chenopodium rubrum</i>	L.	<i>Rudbeckia serotina</i>	Nutt.
<i>Cicuta bulbifera</i>	L.	<i>Rumex maritimus</i>	L.
<i>Cirsium arvense</i>	(L.) Scop.	<i>Rumex occidentalis</i>	S. Wats.
<i>Crepis tectorum</i>	L.	<i>Sagittaria cuneata</i>	Sheld
<i>Eleocharis sp.</i>	(L.) R. & S.	<i>Salix gracilis</i>	Anderss.
<i>Epilobium glandulosum</i>	Lehm.	<i>Scirpus caespitosus</i>	L.
<i>Equisetum variegatum</i>	Schleich	<i>Scirpus microcarpus</i>	Pers.
<i>Erysimum inconspicuum</i>	(Wats.) MacM.	<i>Scirpus validus</i>	Vahl.
<i>Galeopsis tetrahit</i>	L.	<i>Scutellaria lateriflora</i>	L.
<i>Galium trifidum</i>	L.	<i>Scutellaria galericulata</i>	L.
<i>Geum aleppicum</i>	Jacq.	<i>Setaria vividis</i>	(L.) Beauv.
<i>Geum Macrophyllum</i>	Willd.	<i>Sium suave</i>	Walt.
<i>Glyceria grandis</i>	S. Wats.	<i>Solidago canadensis</i>	L.
<i>Glyceria striata</i>	(Lam.) Hitchc.	<i>Sonchus arvensis</i>	L.
<i>Habenaria hyperborea</i>	(L.) R. Br.	<i>Sparganium eurycarpum</i>	Engelm
<i>Heracleum lanatum</i>	Michx.	<i>Stachys palustris</i>	L.
<i>Impatiens biflora</i>	Walt.	<i>Stellaria crassifolia</i>	Ehrh.
<i>Juncus alpinus</i>	Vill.	<i>Taraxacum officinale</i>	Weber
<i>Juncus balticus</i>	Willd.	<i>Thlaspi arvense</i>	L.
<i>Juncus dudleyi</i>	Wieg.	<i>Trifolium repens</i>	L.
<i>Juncus filiformis</i>	L.	<i>Typha latifolia</i>	L.
<i>Juncus nodosus</i>	L.	<i>Urtica dioica</i>	L.
<i>Lemna minor</i>	L.	<i>Vicia americana</i>	Muhl.
<i>Lycopus americanus</i>	Muhl.	<i>Amaranthus retroflexus</i>	L.



Figure A 3.1. Meadow 1 Age 9 years Area 7834 m²

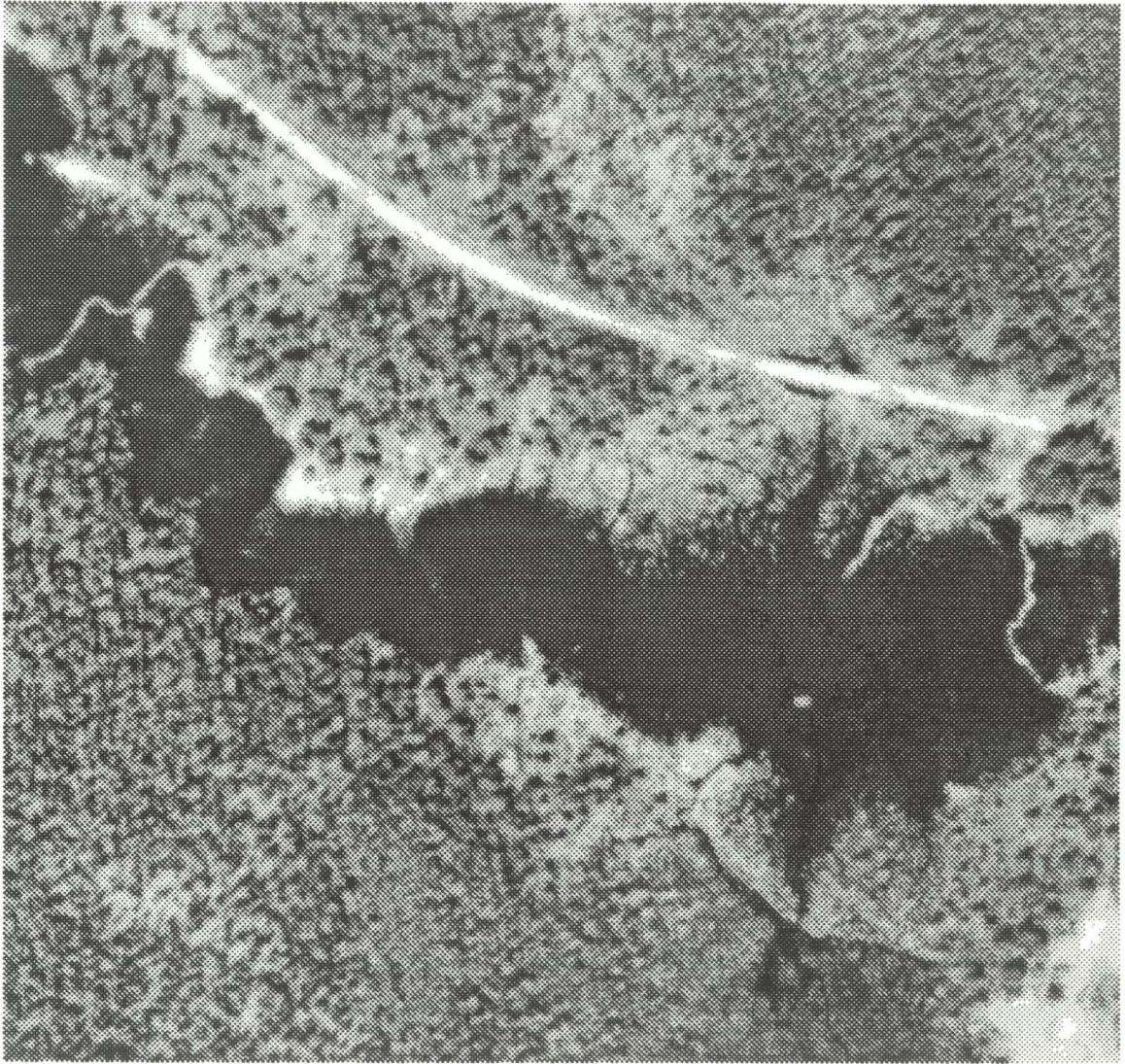


Figure A 3.2. Meadow 2 Age 9 years Area 12909 m²



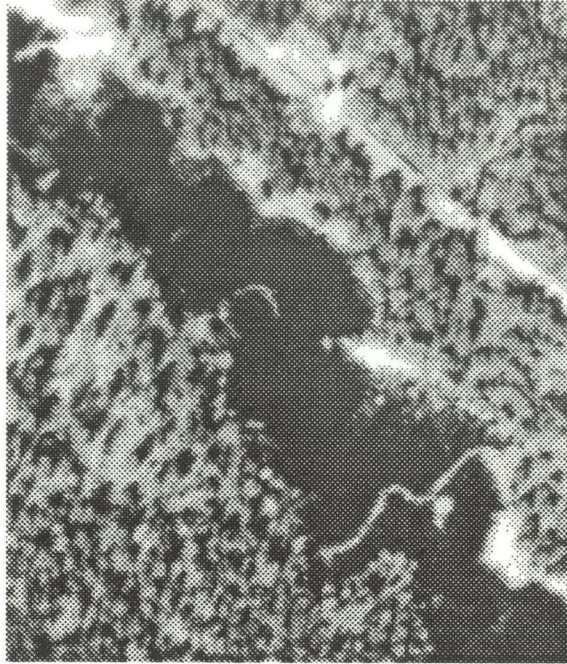


Figure A 3.3. Meadow 3 Age 6 years Area 5821 m²



Figure A 3.4. Meadow 5 Age 21 years Area 6543 m²

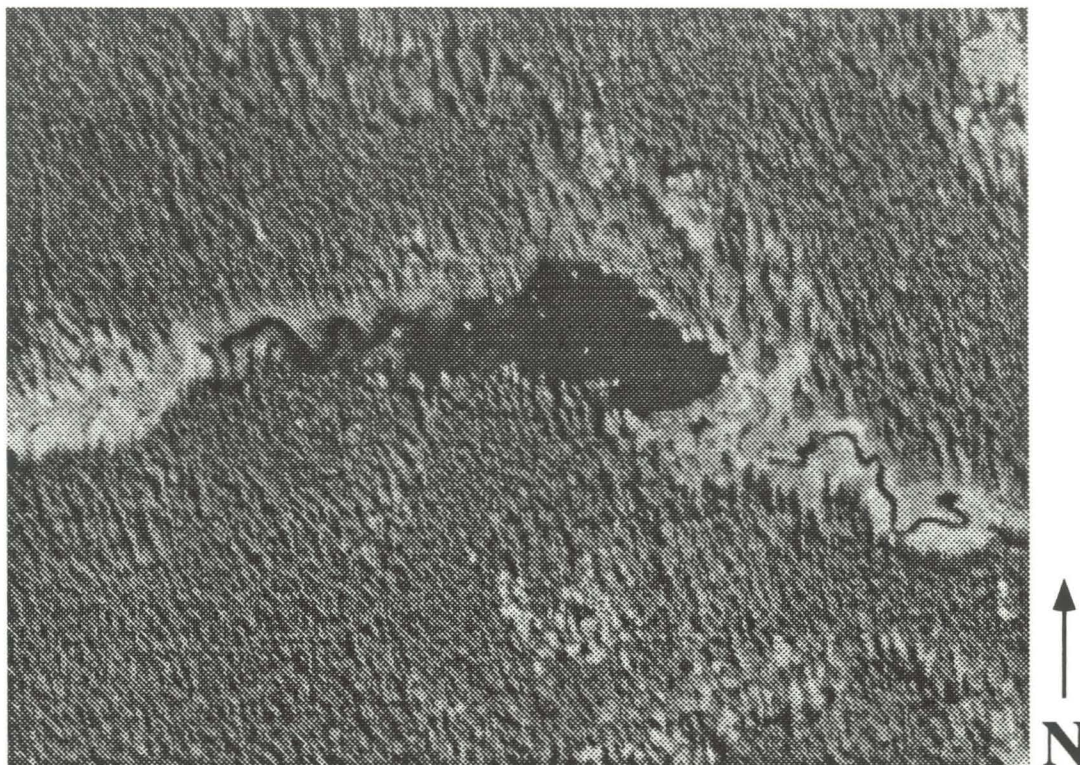


Figure A 3.5. Meadow 7 Age 9 years Area 14792 m²

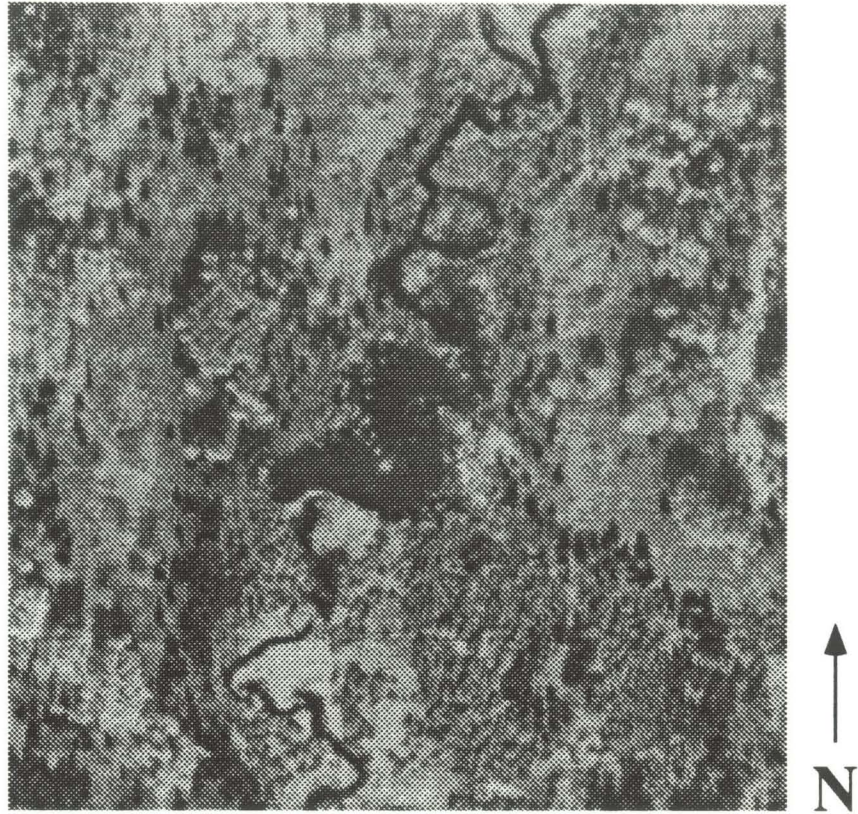


Figure A 3.6. Meadow 8 Age 22 years Area 15636 m²

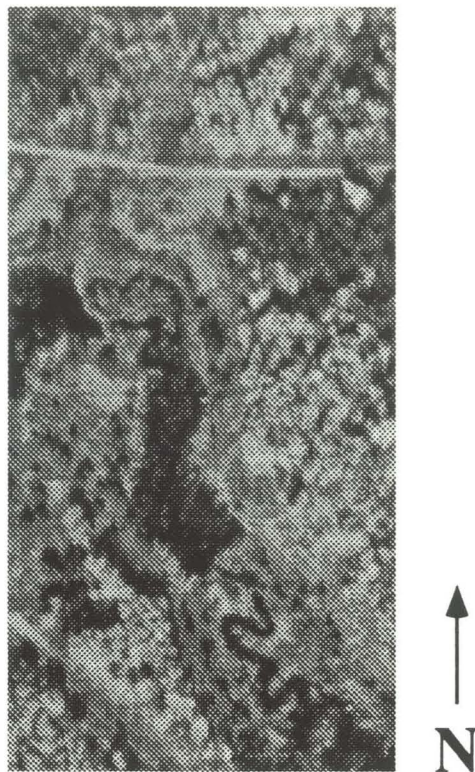


Figure A 3.7. Meadow 11 Age 6 years Area 3867 m²

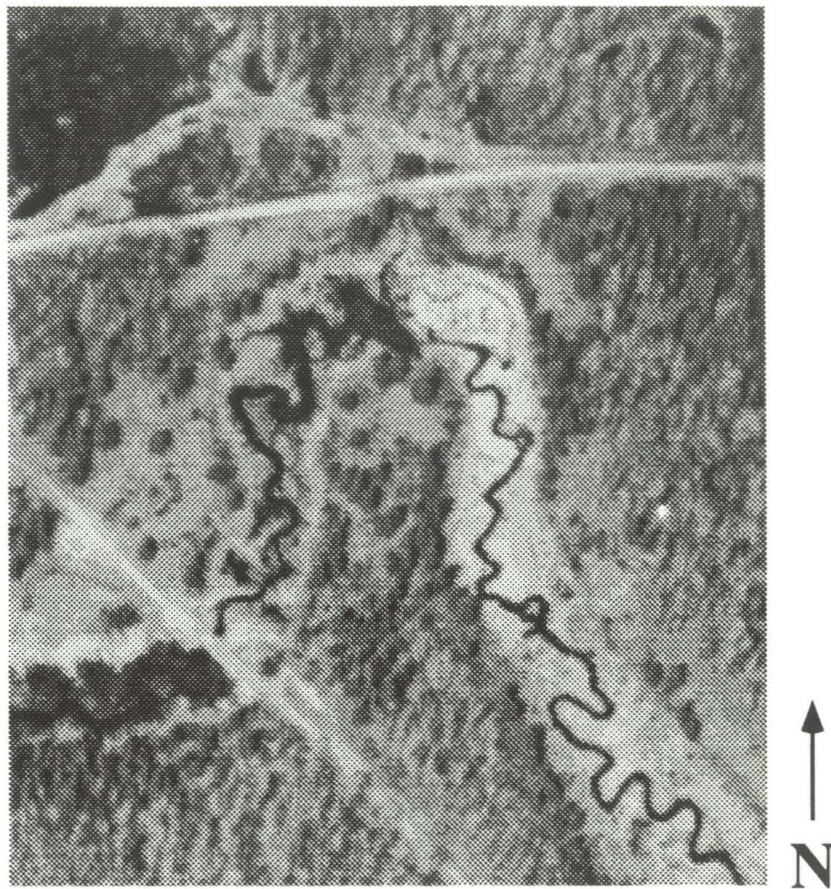


Figure A 3.8. Meadow 12 Age 6 years Area 2265 m²

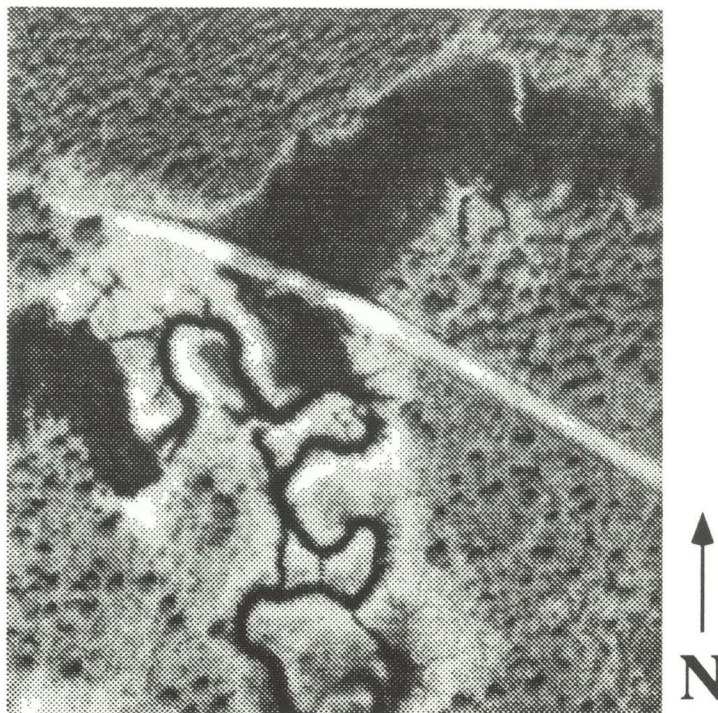


Figure A 3.9. Meadow 14 Age 9 years Area 1815 m²



Figure A 3.10. Meadow 15 Age 6 years Area 22633 m²

