THE ECOLOGY OF OPUNTIA FRAGILIS IN THE BOREAL FOREST REGION OF SOUTHEASTERN MANITOBA

by

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Submitted in partial fulfillment
of the requirements for the
degree of
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ABSTRACT

The distribution of Opuntia fragilis (Nutt.) Haw. in the Boreal Forest Region of southeastern Manitoba was compiled from herbaria, literature, and poster surveys. Eleven colonies were verified, from Indian Bay ($49^{0}37'$N, $95^{0}12'$W) to Bissett ($51^{0}02'$N, $95^{0}41'$W), most on the Winnipeg River system.

The habitat was described from data collected May - September 1980 at seven sites. The cactus occurred on sloping, south-facing outcrops on waterways. It was found 3 - 4 m above the water level in shallow, acidic, nutrient-poor organic soils. A temperature profile through the Bird River valley site ($50^{0}25'$N, $95^{0}41'$W) showed that the microclimate on these outcrops was warmer and drier than that in the surrounding forest.

The morphology of one-year-old pads of O. fragilis varied among the seven sites. This variation was absent from new pads produced after one year of uniform conditions. Morphology was not significantly correlated with soil or physiographic characters of the sites. Pad length appeared to be related to light intensity.

The effects of propagule dispersal, establishment, and maintenance on the distribution of O. fragilis in this region were tested at Bird River from May 1981 - October 1982. Because the cactus propagates vegetatively, the propagules used were stem units (pads). Mark and recapture, flotation experiments, and field observations indicated three potential dispersal mechanisms. In order of increasing risk to survival, they are:

1. geochory, which dispersed pads locally and introduced them into the river.
2. hydrochory, which dispersed pads over long distances, but restricted their spread to waterways.
3. epizoochory, which also functioned over long distances, given suitable vectors (e.g. humans).

Marked pads were planted in habitats to which they might be dispersed. After one year, establishment was significantly greater ($P < 0.05$) on south-facing outcrops than on north-facing or forest sites.

Censuses (1979 - 1982) of an established colony indicated that pad numbers were increasing by 30% per year. Approximately 6% of the pads were dispersed from the outcrop.

The original date of arrival in Manitoba is unknown, but three time periods could be hypothesized: 9000 - 7500 years BP, 7500 - 4000 BP, or 4000 - 0 BP. The present distribution of O. fragilis appears be be maintained by hydrochory and/or epizoochory along canoe routes. The cactus is both habitat and dispersal limited.

The successional sequence on three outcrops containing O. fragilis was examined using physiography and species cover. Data were collected from June - August 1982 on five 10 m line transects at each site. A successional sequence of species was predicted, based on their life-forms, strategies, and contribution to soil formation. Preliminary ordinations using reciprocal averaging/weighted averaging hybrids indicated that substrate depth was the major factor determining the species gradient, hence substrate depth was used to order samples in weighted averaging ordinations. The resulting species sequence was positively correlated with the predicted sequence ($P < 0.05$). The stages of the sequence were: (0) bare rock/pioneer lichen mat, (1) primary moss mat, (2) secondary moss and lichen mat, (3) tertiary mat, (4) stress-tolerant perennials, (5) perennial grasses and sedges, and (6) chamaephytes and phanerophytes. The species composition of stages 0 - 3 was consistent at all three sites. Variation in subsequent stages was presumably due to propagule availability. This sequence was generally similar to that of Clements (1963) but local variations in pattern and rate of spread were related to factors which altered the rate of soil accumulation: slope, aspect, rock surface features, and disturbance.

Opuntia fragilis, a stress-tolerant perennial, was the first vascular plant to colonize secondary (occasionally tertiary) mats, where it was positively associated with Tortula ruralis ($P < 0.05$). Cactus vigour was not correlated with soil or physiography ($P > 0.05$).

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CHAPTER ONE

Introduction

A colony of *Opuntia fragilis* (Nuttall) Haworth in the Boreal Forest Region (*sensu* Rowe 1972) of southeastern Manitoba has been observed annually since ca. 1966. The colony, located on Bird River, was restricted to two outcrops but was absent from the forest and apparently similar outcrops nearby. Propagation appeared to be entirely by vegetative pads.

This study was designed to determine whether this colony was unique, and to examine the ecology of a supposedly prairie species in a boreal habitat. My aims were:

1. to report the distribution and habitat of *Opuntia fragilis* in the Boreal Forest Region of southeastern Manitoba (Chapter II). The help of local naturalists was enlisted to locate previously unknown cactus colonies. Where possible, these were verified by specimens. A selection of seven colonies was studied to compile a habitat description.
2. to examine the influence of dispersal, establishment, and maintenance on distribution and abundance (Chapter III). Individual components of distribution were tested to determine whether the species was restricted to certain habitats.
3. to compare successional sequences and ecological positions of *O. fragilis* at three sites (Chapter IV). Succession on outcrops did not appear to follow the spatial continuum pre-

dicted by Clements (1963). Instead, the vegetation occurred in discrete patches. Vegetation cover and physiography were analyzed to define a successional sequence, and to predict the position of *O. fragilis* in the sequence.

The answers to these questions may provide insight into the cactus' requirements and history.

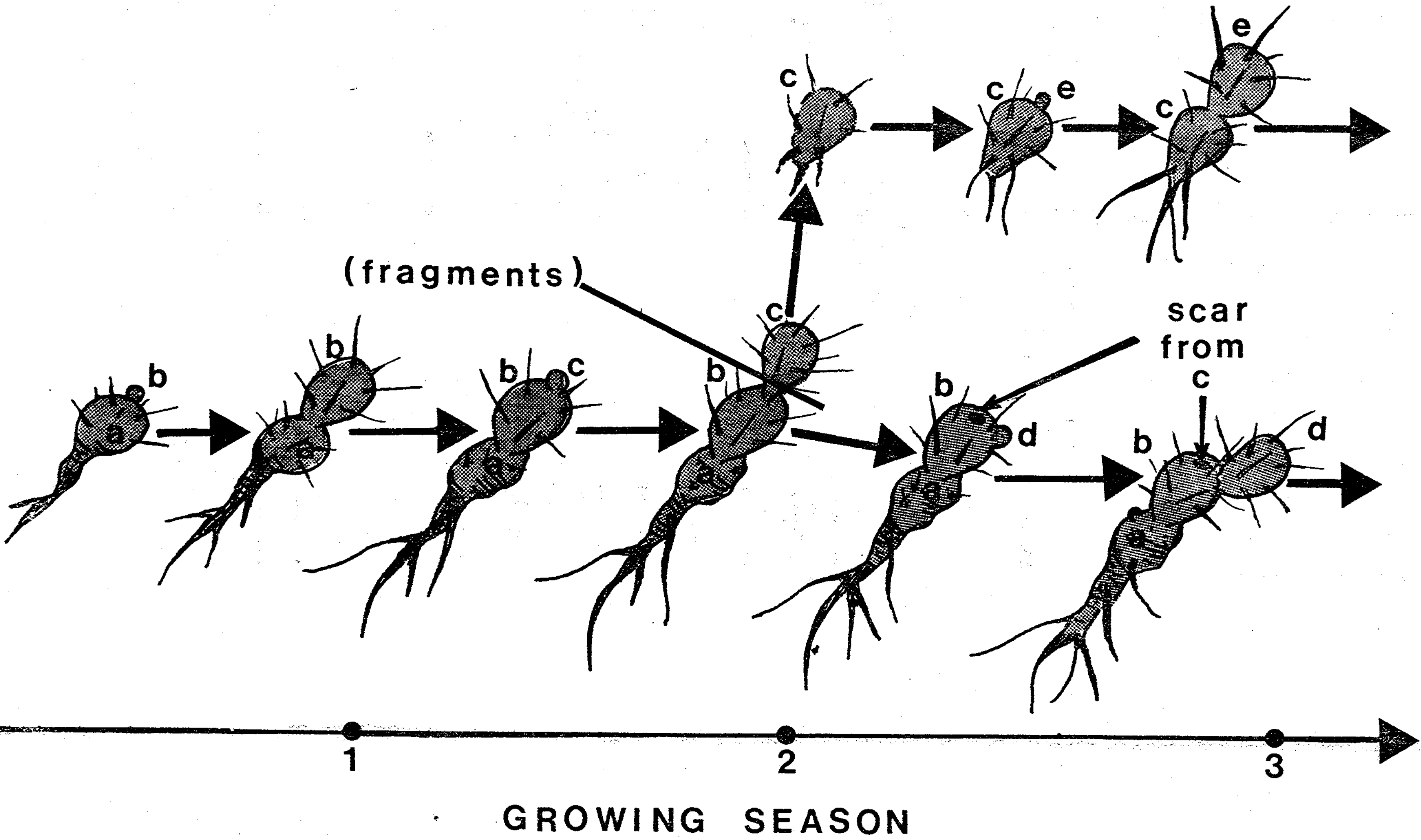
In order to describe the ecology of *Opuntia fragilis* in southeastern Manitoba, some information on its biology was useful in understanding its strategy of reproduction and spread. The general characteristics of the study region, especially its history, provided information on the possible history of the cactus distribution.

Description of Species

Vegetative morphology

Opuntia fragilis, or Brittle prickly pear cactus, is so named because the stem is easily separated into individual pads (c.f. "modules" *sensu* Harper 1978). The stem consists of a series of cylindrical succulent photosynthetic pads each up to 4 cm long (Benson 1974, Clark 1981), arranged in a decumbent chain (Fig. 1.1). Each terminal pad produces one (occasionally two) new pads from its apical meristem each spring, hence the chain lengthens annually in a linear fashion. Lateral meristems produce new pads or adventitious roots. Surrounding each meristematic region on the surface of the pad is a cluster of hair-like glochids and up to 9 spreading barbed spines (see e.g. Makuchan 1979, Clark 1981, Harms 1983). Each meristematic region, including spines, glochids, and deciduous scale-like leaf, is termed an areole.

Figure 1.1: Morphology of a stem of *Opuntia fragilis*, showing pattern of growth over three growing seasons. Individual pads are identified by letters a - e. Pad c breaks off the main stem in the second growing season to form a separate plant.


a
b
c
d
e
(fragments)
scar from c
0
1
2
3
GROWING SEASON

Vegetative Anatomy

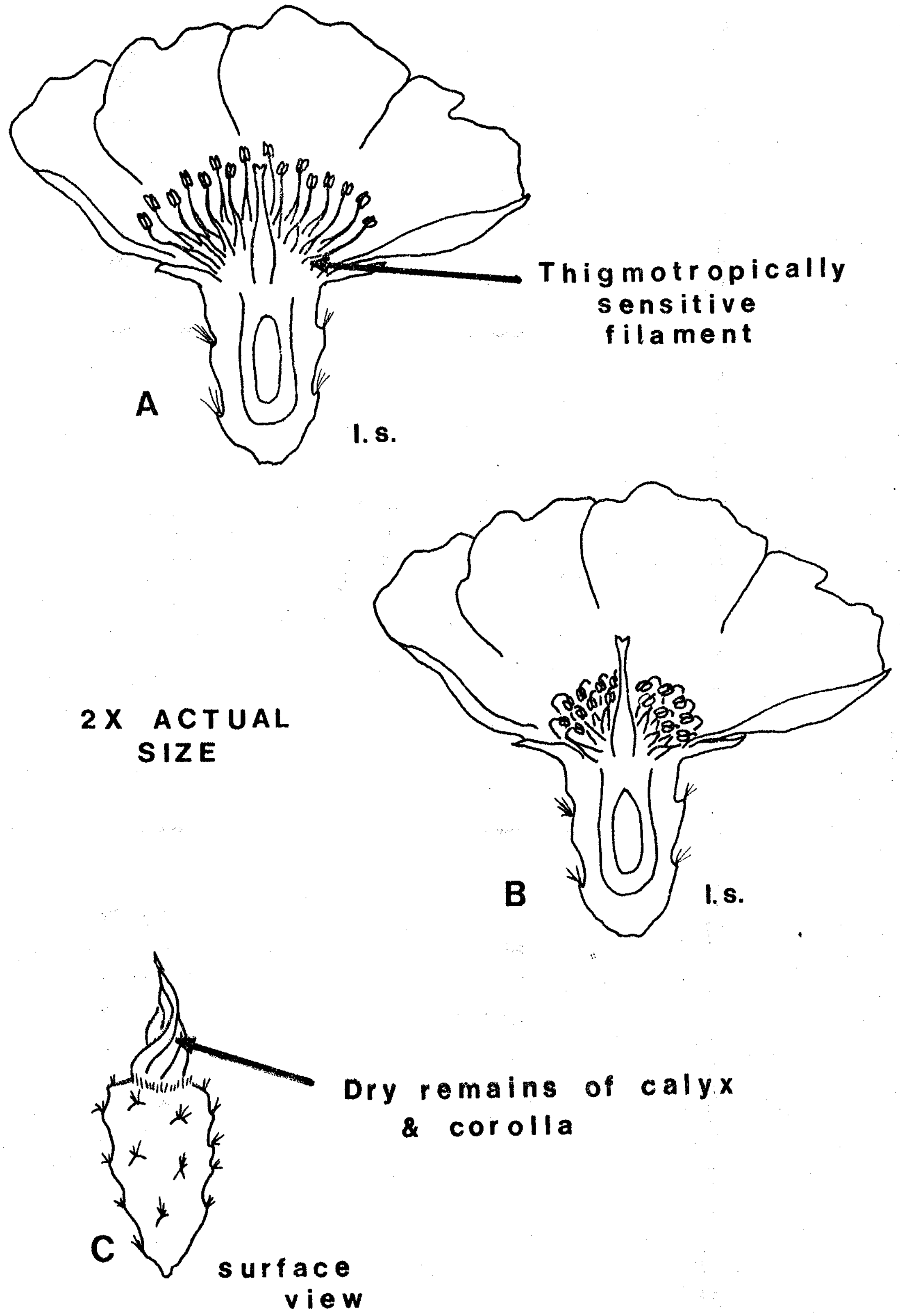
Anatomy has been described by Clark (1981). The thick cuticle and multi-layered epidermis of the pad are perforated by numerous stomata. The mucilaginous interior of the pad contains crystals of calcium oxalate, mucilage cells, true vessels and vascular tracheids with helical thickenings (unique to the Cactaceae), and abundant water-storing parenchyma. The helical thickenings provide elasticity, while the tracheids function in support. These features allow the plant to respectively survive, and recover from, drought and loss of turgor.

Reproductive Chacteristics

Opuntia fragilis flowers in early to mid-summer (Benson 1974). In the Bird River area of southeastern Manitoba, the flowering season occurred in late June. The flowers (Fig. 1.2a) are epigynous, 3.5-5.0 cm in diameter, bright yellow, tinged with red. The stamens are thigmotropically sensitive, a generic character. The lower portion of the filament is widened and bends rapidly inward when triggered (i.e. by an insect). The anthers contact the style below the stigma, trapping the insect as in a cage (Fig. 1.2b). As the insect escapes between the filaments, it becomes dusted with pollen (Toumey 1899). This is believed to promote cross-fertilization (Toumey 1899, Grant and Hurd 1979, Parfitt and Peckett 1980). The incurved filaments

Figure 1.2: Reproductive structures of <u>Opuntia fragilis</u>.

(A) Longitudinal section through flower, showing stamens in open position.
(B) Stamens incurved.
(C) Fruit with persistent corolla and calyx.


Thigmotropically sensitive filament
A
l.s.
2X ACTUAL SIZE
B
l.s.
Dry remains of calyx & corolla
C
surface view

have trapped nitulid beetles (not effective pollinators) and medium to large polylectic bees (Toumey 1899, Grant and Hurd 1979). Thigmotropism has been observed at the Bird River colony and in the laboratory with collected flowers. No insect visitors have been seen at this site.

The fruits are indehiscent, dry, woody, and have apical rims of spreading barbed spines (Fig. 1.2c) which aid in dispersal. Seeds reach maturity 2-3 months post anthesis, and are flattened, 0.5-0.6 cm long, and bone-coloured. Many are sterile or parasitized by insect larvae, and are then thin and papery (Benson 1974). Fruits from Bird River, Bissett, Big Whiteshell, and Spruce Woods were examined from 1979-1981, but no viable seeds were found.

The chromosome number for this species is unknown, however the genus *Opuntia* is known to have a basic chromosome number (x) of 11, and various species appear to be polypoids of this, i.e. from 3x-12x (Pinkava *et al*. 1973). *Opuntia fragilis* hybridizes with *O. polyacantha* Haw. in the northwestern U.S. (Benson 1974).

Like many other species in this genus, *Opuntia fragilis* produces few seeds and relies on vegetative propagation throughout its range (Grant and Hurd 1979). Mature terminal pads are prone to separation from the stem, especially in mid-summer, the season of maximum turgor. This stem segmentation, the presence of barbed spines (which aid in anchorage and dispersal, c.f. Toumey 1899, van der Pijl 1969), and adventitious root production have probably contributed to its spread in rangeland (Toumey 1899, Bunting *et al*. 1980), and into other habitats (e.g. the Boreal Forest Region).

Distribution

The distribution of Opuntia fragilis covers the general region of the Great Plains. A map of the main range of O. fragilis (Fig. 1.3) was compiled from the major floras of North America; it extends from New Mexico, through northern California, north to the Peace River district of British Columbia and Alberta (DAO 269656), and east through southern Saskatchewan and Manitoba to Ontario. Towards the northeastern edge of its range, distribution becomes patchy. Discrete isolated populations are reported at Kaladar, Ontario (DAO 82194, Beschel 1967), Illinois (Gleason 1923, Sheviak 1979), and Michigan (Reznicek, pers. comm. 1981).

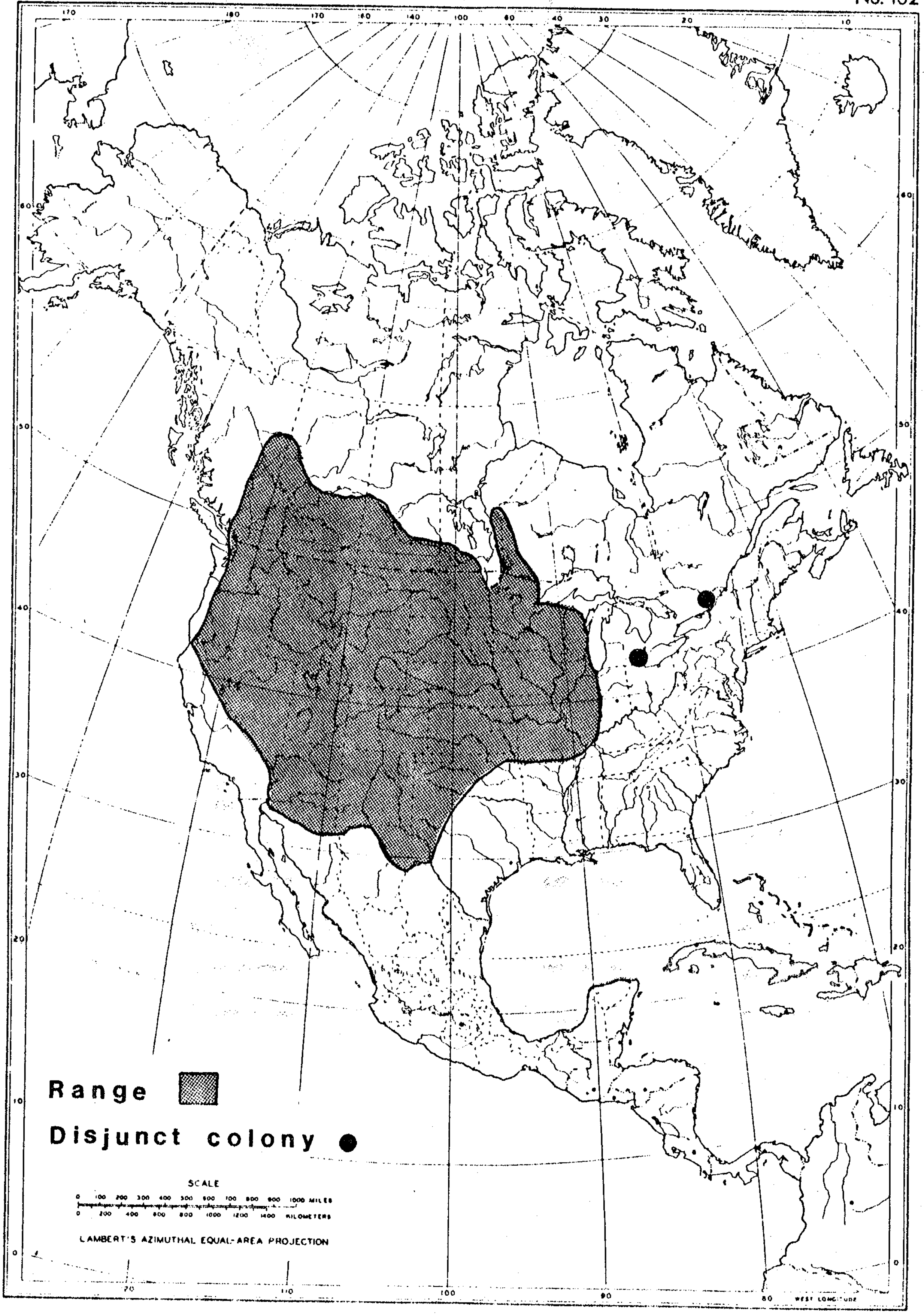
In Canada, Opuntia fragilis has a patchy distribution (Fig. 1.4). It occurs in two different habitats: (a) dry prairies and sandhills, from the southern interior of British Columbia, to southwestern Manitoba; and (b) on rock outcrops in coniferous forests, e.g. on shores and islands in the Straits of Georgia, B.C. (DAO 82236); and on lakeshores in southeastern Manitoba and northwestern Ontario (Scoggan 1978). The colonies on rock outcrops in Manitoba and Ontario fall within the Boreal Forest Region (sensu Rowe 1972).

Description of Study Area

The cactus habitat in the boreal forest is outwardly dissimilar to that of the Great Plains in topography, soil, and vegetation.

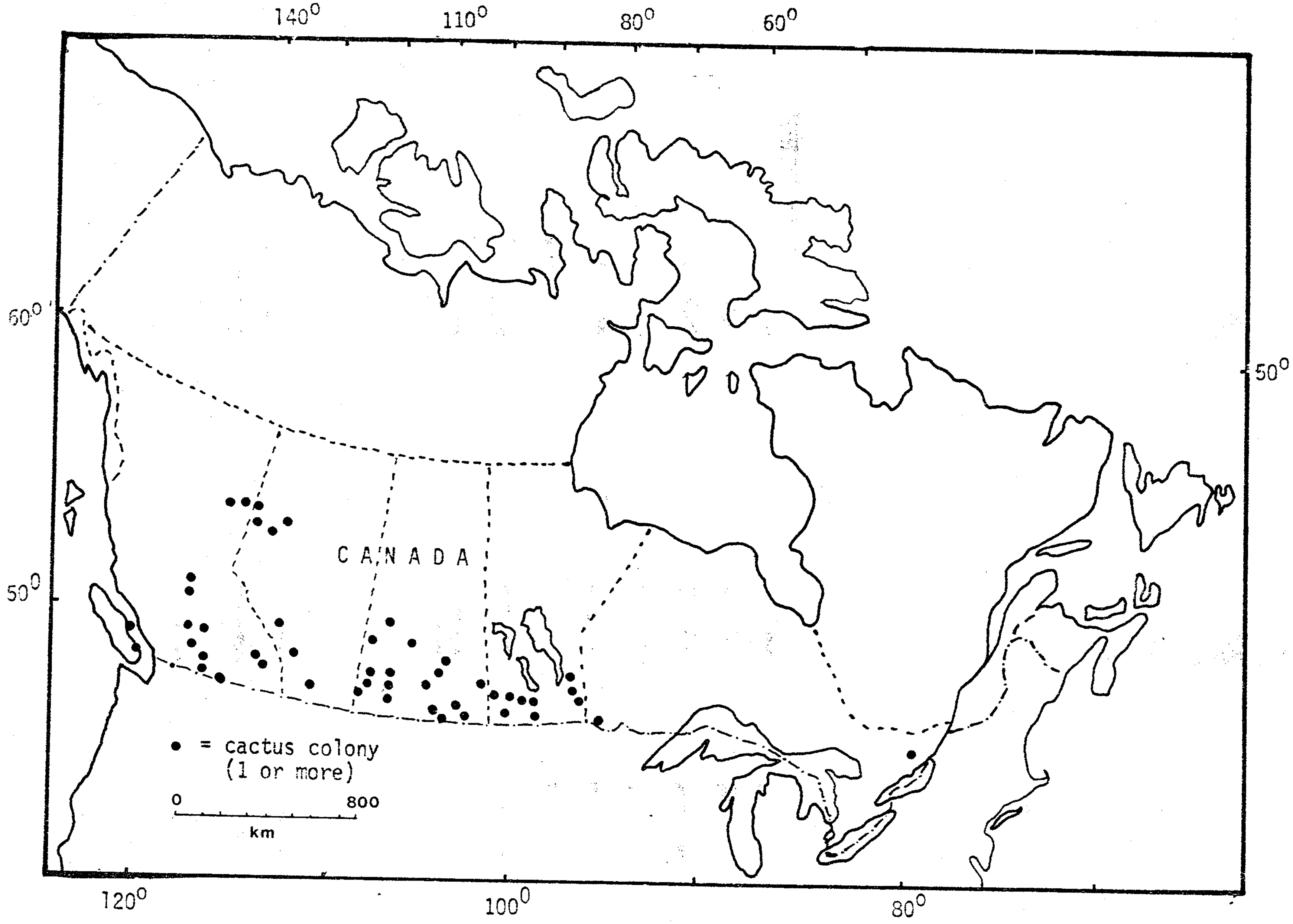
The topography of the Boreal Forest Region of southeastern Manitoba rises from 250 to 330 m above sea level from west to east.

Figure 1.3: Range of _Opuntia fragilis_ in North America.



NORTH AMERICA No. 102

Figure 1.4: Distribution of *Opuntia fragilis* in Canada.


140°
110°
80°
60°
60°
50°
50°
CANADA
● = cactus colony
(1 or more)
0
800
km
120°
100°
80°

Soils are shallow, acidic, and nutrient-poor. They are the result of climate, which slows decomposition; parent material (i.e. weathered granite and/or glacial till); and relief, which promotes erosion and leaching (Smith and Ehrlich 1967). Soils and vegetation types are discontinuous; forested areas are interspersed with bog and bedrock outcrops. Climax forest is composed of *Picea glauca* (Moench) Voss, *Pinus banksiana* Lamb., and *Abies balsamea* (L.) Mill., with local mixtures of deciduous species such as *Betula papyrifera* Marsh. and *Populus tremuloides* Michx. Bogs are characterized by *Sphagnum* spp. with *Picea mariana* (Mill.) BSP. and *Larix laricina* (DuRoi) Koch. Outcrop vegetation is variable and is discussed in Chapters II and IV.

Post Glacial History

15,000-13,500 years BP. During the Wisconsin Ice Age, Manitoba was covered by a glacial ice sheet which extended into the northern U.S.A. (Terasmae 1973). The previous flora and fauna were displaced to refugia in southern and central U.S.A. (Terasmae 1973, Scudder and Reveal 1981).

13,500-13,000 BP. The climate began to warm. Meltwater formed Glacial Lake Agassiz I, covering southern Manitoba and parts of Saskatchewan and Ontario (Ritchie 1976). Initially the lake drained south into the Mississippi River basin. As the ice receded, the lake drained east into the Lake Superior basin (Zoltai 1967). Glacial till accumulating on the melting ice was colonized by spruce forest (Ritchie 1976).

13,000-9,900 BP. The climate continued to warm. Grassland colonized southwestern Manitoba (Mott 1973, Ritchie 1976), but southeastern Manitoba remained flooded.

9,900-9,000 BP. After a brief period of glacial readvance, the climate warmed again. Meltwater formed Glacial Lake Agassiz II (Löve 1959) which drained south and southwest into Glacial River Warren (Matsch and Wright 1967, Zoltai 1967). The spruce forest was invaded by pine (Buchner 1979, 1981). Löve (1959) proposed the arrival of "eastern elements" during this period, including *Selaginella rupestris* (L.) Spring, *Prunus pumila* L., *Saxifraga virginiensis* Michx., *Rhus glabra* L., and *Quercus macrocarpa* Michx. However, Ritchie (1976) dated the arrival of *Q. marcrocarpa* at 6,500 BP.

9,000-7,500 BP. Lake Agassiz II drained east and northeast through successively lower channels as the ice retreated (Zoltai 1967). Southeast of the lake may have been pine savannah (Buchner 1981) while grassland extended south and southwest (Nichols 1969).

7,500-4,000 BP. A warm dry climatic period, the Altithermal (*sensu* Antevs 1948), caused water levels to drop. Grassland reached its maximum extensions, north to Riding Mountain (Ritchie 1976) and perhaps east to the Winnipeg River (Buchner 1981). Boreal forest was similar to its modern composition but lay 100-175 km north of its present boundary (Ritchie 1976). "Western elements", including *Andropogon gerardi* Vit., *Heuchera richardsonii* R.Br., *Allium stellatum* Fraser, and *Opuntia fragilis*, may have arrived (Löve 1959).

4,000-2,500 BP. The climate cooled to present conditions, and Lake Agassiz II began to drain north into the Nelson River (Zoltai 1967). Grassland retreated and the boreal forest reached its present southern limit. Plains Indians began to penetrate the boreal forest (Buchner 1981). Vestiges of earlier plant assemblages persisted in isolated sites, e.g. stands of oak savannah on south-facing slopes in southwestern Manitoba (Ritchie 1976). Altithermal vegetation may persist on protected sites (e.g. islands, c.f. Wright and Heinselman 1973).

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CHAPTER TWO

Distribution, Habitat, and Variation of *Opuntia fragilis* in Southeastern Manitoba

ABSTRACT

The distribution of *Opuntia fragilis* (Nutt.) Haw. in the Boreal Forest Region of southeastern Manitoba was compiled from herbaria, literature, and poster surveys. Eleven colonies have been verified from Indian Bay (49°37'N, 95°12'W) to Bissett (51°02'N, 95°41'W), most on the Winnipeg River System.

The habitat was described from data collected May - September 1980 at seven sites. The cactus occurred on sloping, south-facing outcrops on waterways. It was found three to four m above the water level, on shallow, acidic, nutrient - poor soils in moss mats. A temperature profile through the Bird River valley site (50°25'N, 95°41'W) showed that the microclimate on these outcrops was warmer and drier than that in the surrounding forest.

The morphology of one-year-old pads of *O. fragilis* varied among the seven sites. This variation was absent from new pads produced after one year of uniform conditions. Morphology was not significantly correlated with soil or physiographic characters of the sites. Pad length appeared related to light intensity.

CHAPTER TWO

Distribution, Habitat, and Variation of *Opuntia fragilis* in in Southeastern Manitoba

Introduction

Preliminary studies on a long-known colony of *Opuntia fragilis* at Bird River, Manitoba (50°25'N, 93°38'W) revealed the existence of other colonies in the Boreal Forest Region (*sensu* Rowe 1972) of southeastern Manitoba. Colonies were at least 70km east-northeast of the edge of the species' main grassland distribution (see Fig. 1.3, Chapter 1). The distribution of isolated cactus colonies suggested the following questions:

1. What is the distribution of *O. fragilis* in the Boreal Forest Region of southeastern Manitoba? Is it a rare species in this region?
2. What are the biotic and abiotic features of the habitat of *O. fragilis* in this region?
3. Is there any morphological variation among plants from different isolated sites?

General Site Description

Landforms. The study area was located in the Lower English River Section of the Boreal Forest Region (Rowe 1972), on the heavily glaciated Canadian Shield. Altitude ranged from 250 to 330 m above sea level, west to east.

Climate. Data on the humid continental climate of this region were obtained from meteorological stations near the study sites (Fig. 2.1). Greatest precipitation (Anon. 1975 a) and highest temperature (Anon. 1975 b) occurred in July (Fig. 2.2 A). Annual number of frost free days varied from 110 to 128 days per annum (Hemmerick and Kendall 1972), with no frost from June-August (Fig. 2.2 B).

Soil. The Indian Bay Soil Complex of the area was characterized by "outcroppings of granitoid rocks and marked local relief ... associated with ... (localized) Podzolic, Gleysolic, and Organic soils (which) are highly variable as to mode of deposition, mineralogical composition, drainage, and stoniness" (Smith and Ehrlich 1967).

Vegetation. Species composition was also discontinuous, associated with local soil features. *Pinus banksiana* Lamb., *Picea glauca* (Moench) Voss, and *Abies balsamea* (L.) Mill. grew on the deeper dry soils. Bogs were characterized by *Sphagnum* spp. and *Picea mariana* (Mill.) BSP. Outcrop vegetation varied, but was generally xerophytic.

Methods and Materials

Distribution in Southeastern Manitoba

Distribution records were compiled by: (1) field observation, (2) contact with knowledgeable people, e.g. local naturalists, park rangers, and prospectors, and (3) a poster survey.

Figure 2.1: Location of seven cactus study sites and meteorological stations from which climatic data were obtained.

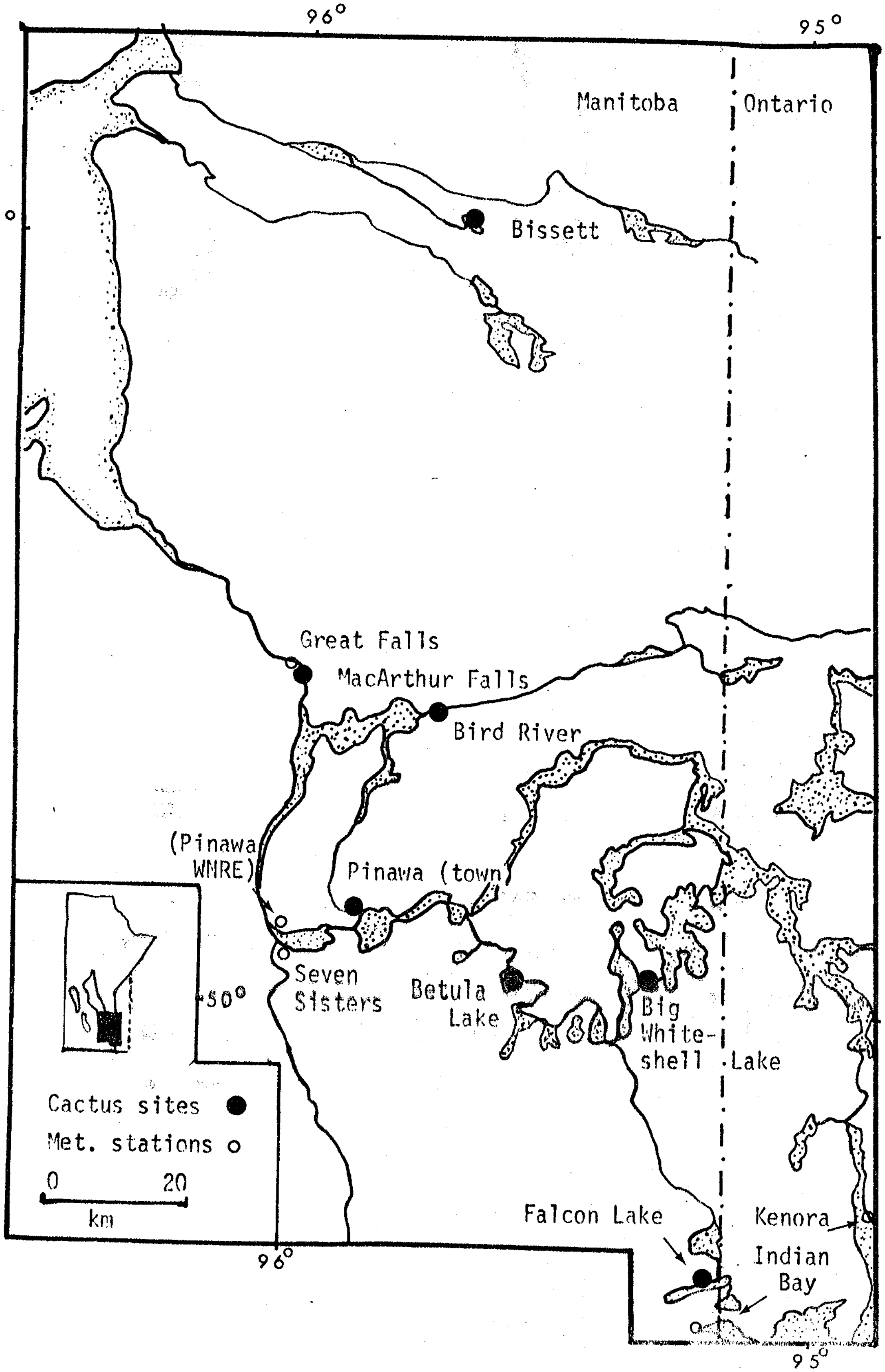
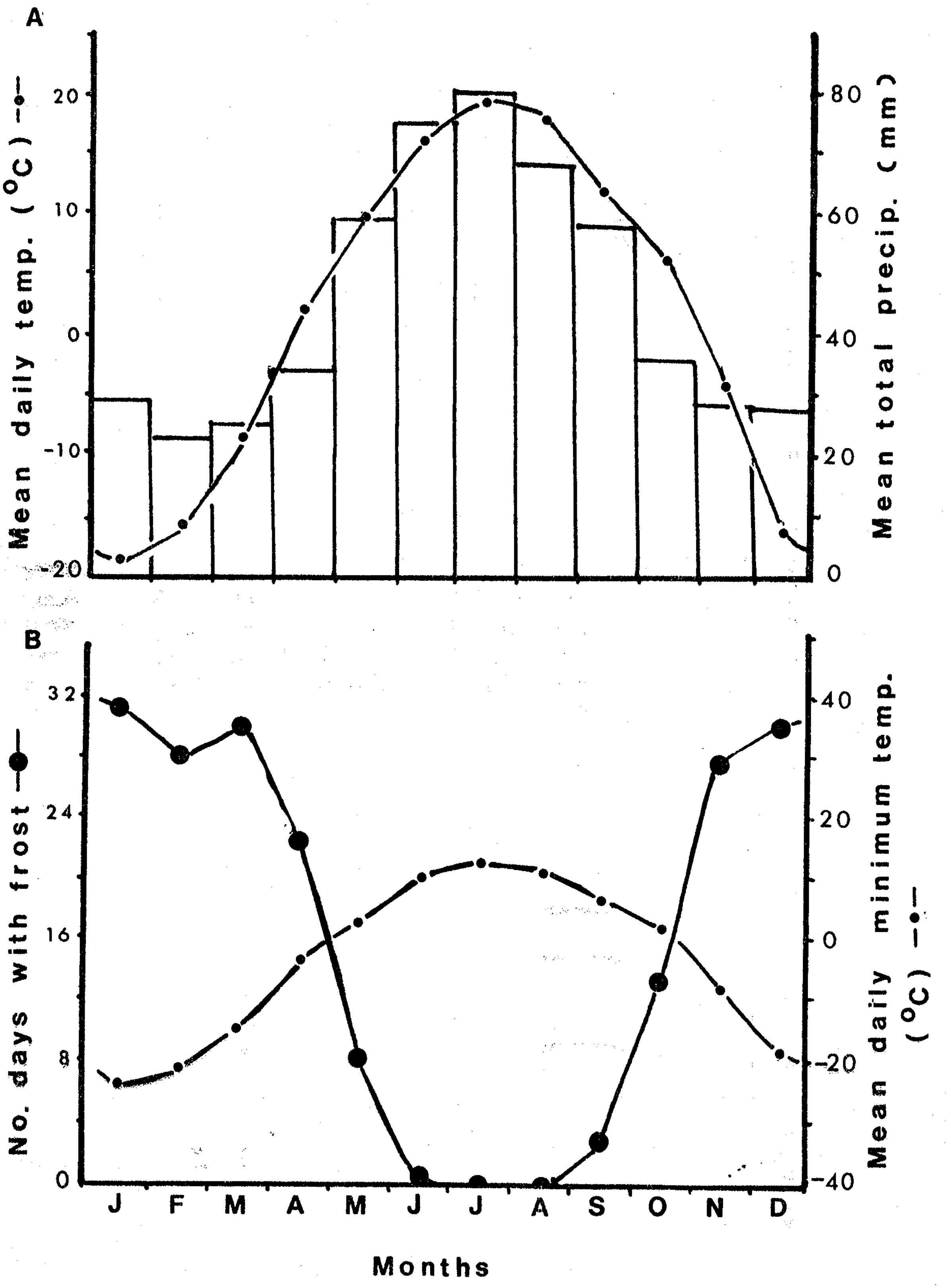

96°
95°
Manitoba
Ontario
51°
Bissett
51°
Great Falls
MacArthur Falls
Bird River
(Pinawa
WNRE)
Pinawa (town)
Seven
Sisters
Betula
Lake
Big
White-
shell
Lake
50°
50°
Cactus sites ●
Met. stations ○
0
20
km
Falcon Lake
Kenora
Indian
Bay
96°
95°

Figure 2.2: Climatic means for study area in southeastern Manitoba.
(A) Mean daily temperature (Anon. 1975 b) and mean total precipitation (Anon. 1975 a), and
(B) Number of days with frost (Hemmerick and Kendall 1972) and mean daily minimum temperature (Anon. 1975 b), by month.


A
Mean daily temp. (°C)
20
10
0
-10
-20
Mean total precip. (mm)
80
60
40
20
0
B
No. days with frost
32
24
16
8
0
Mean daily minimum temp. (°C)
40
20
0
-20
-40
J
F
M
A
M
J
J
A
S
O
N
D
Months

Posters requesting reports of _Opuntia fragilis_ were mailed to schools, post offices, etc. in 77 locations throughout rural Manitoba (Appendix 2.1). Correspondents were asked to locate the colonies on detailed maps of their area. Where possible, I verified these colonies during the summers of 1979-1981.

Habitat Description, Based on Selected Study Sites

Seven representative sites were sampled to describe the cactus habitat (Fig. 2.1): Falcon, Big Whiteshell, Betula Lakes, Bird River, MacArthur Falls, and Bissett. The selection criteria were that sites should:

1. have large colonies of cacti,
2. represent the known latitudinal range of _Opuntia fragilis_ in southeastern Manitoba,
3. represent the different river systems on which the cacti are found,
4. have minimal human disturbance, and
5. be accessible.

The habitat description was compiled from individual site descriptions (summer 1980) and published data.

Abiotic data were collected as follows:

1. Physiography. Altitude and glacial deposits for each site were obtained from cartographic references. Recent history of disturbance was obtained verbally from residents. Aspect was recorded using a compass. Angle of slope and vertical distance above water were estimated using meter sticks and a measuring tape.

2. Climate. Temperatures were measured across the Bird River valley on a north-south transect (96m horizontally), which bisected a cactus colony. Twelve maximum/minimum thermometers were used to record daily extremes during the period of maximum spring growth (preliminary studies, 1980), from May 27-29, 1982. This included sunny and cloudy days. A profile of the valley was drawn.

3. Soil. Two soil samples, approximately 10 x 10 x 10 cm, were collected from beneath cactus colonies, and two from the adjacent boreal forest at each site (see Table 2.3). Samples included the litter layer and were stored frozen. Conductivity, pH, organic content, and macronutrient concentrations were determined using the standard techniques (McKeague 1978) of the Manitoba Provincial Soil Testing Labortory. Bulk density was calculated using the equation (Jeffrey 1970):

$$\underset{(\text{g/ml})}{\text{Bulk density}} = 1.482 - 0.6786 \log (\%\ \text{organic content}).$$

Nutrient content was converted from ppm to kg/ha using the equation:

$$\text{ppm} \times 2 \times \frac{\text{bulk density}}{1.3\ \text{g/ml}} \times \frac{\text{sample depth}}{15.3\ \text{cm}} = \text{kg/ha}$$

(McGill 1981, pers. comm.)

This conversion to content per area estimated the nutrient availability in shallow discontinuous soil deposits (Racz 1981, pers. comm.). The Student's t-test (Sokal and Rohlf 1969) was used to test differences between means of forest and outcrop soils.

Biotic data were collected as follows:

1. Outcrop and forest vegetation. Vegetation was sampled May-September 1980, and voucher specimens deposited in UWPG. At each site, percent cover of all plant species was sampled at four locations (two on outcrops and two in the boreal forest) using nested quadrats of 0.09m^2 (0.3 x 0.3 m), 1m^2 (1.0 x 1.0 m), and 16m^2 (4.0 x 4.0 m). Quadrat sizes were selected to detect microcommunities of lichens and mosses, herbs and forbs, and shrubs and trees, respectively (c.f. Kershaw 1973). The 0.09m^2 samples were omitted in the forest as the thallophytic microcommunities were observed to be homogeneous. A species list was compiled for vegetation encountered in the quadrats (Appendix 2.3); authorities for all species are noted on the species list.
2. Cactus colonies. The number of colonies per outcrop and the number of pads per colony were recorded at each site. Fresh weight and dimensions (length, width, and depth) of 20 one-year-old pads from each site (excluding Pinawa) were recorded. The pads were placed on a mix of equal parts potting soil, peat, and sand in an environmental chamber. Over a period of seven months, the temperature and day length were gradually reduced to 0°C and 6hr, then increased to 20° and 18hr, respectively. Pads were placed outdoors in full sun in May 1981, and harvested in September 1981. Fresh weight, dry weight (biomass), and dimensions of the field-collected pads (1980, 1981) and their progeny (1981) were tested for variation among sites using

analysis of variance and the Student's t-test (Sokal and Rohlf 1969). Colony size was tested for correlation with the soil variables.

Results

Distribution

Of the colonies reported from the survey (Appendix 2.4), all fell within the Lower English River or Nelson River Sections of the Boreal Forest Region. They ranged from Indian Bay (49°37'N, 95°12'W) to Norway House (54°00'N, 97°48'W). All occurred on rock outcrops on the shores of rivers or lakes.

Habitat Description, Based on Selected Study Sites

The seven study sites (Fig. 2.1) were all exposed, south-facing slopes, except MacArthur Falls which had a negligible slope to the north (Table 2.1).

Falcon Lake. On the north shore of Falcon Lake; a triangular granite outcrop, 12 m at its base on the lakeshore and sloping upward to its apex 2 m above the water level; bounded by a small inlet on the east and by deciduous shrubs (e.g. *Prunus virginiana*) and grasses on the west. Cacti were located in several cracks in the rock and in shallow organic deposits in depressions. The site was on a cottage lot but little disturbed.

Big Whiteshell Lake. On the southern shore of an island in north-central Big Whiteshell Lake; cacti were located on a smooth

Table 2.1: Physiographic characteristics of seven study sites.

Site	Location**				Approx.	
	Longitude	Latitude	River System	Altitude** (m)	Size of Outcrop(m^2)	Average Slope
Falcon Lake	49°43'N	95°15'W	Lake of the Woods	300	72	1:6.5
Big Whiteshell Lake	50°06'N	95°20'W	Whiteshell River	300	184	1:6.7
Betula Lake	50°05'N	95°35'W	Whiteshell River	270	36 *	1:2
Pinawa Channel	50°09'N	95°53'W	Winnipeg River	255	125	1:7
Bird River	50°25'N	95°41'W	Winnipeg River	240	120	1:2
MacArthur Falls	50°24'N	96°00'W	Winnipeg River	245	270	1:11
Rice Lake, Bissett	51°02'N	95°41'W	Wanipigow River	260	450	1:3.7

---

* represents size of ledges on which cacti were found. The entire outcrop covered approximately $5km^2$.

** Anon. (1977).

rectangular slab of granite (23 x 8 m) which sloped to the water's edge. The slope was bounded by a dense cover of unidentified grasses and deciduous trees and shrubs (e.g. Quercus macrocarpa) in the east and by a dense cover of mixed deciduous trees and shrubs (e.g. Populus tremuloides and Prunus virginiana) in the west and north. This woodland covered most of the island. The outcrop appeared undisturbed, however there was evidence of human activity on the opposite side of the island.

Betula Lake. On the northeast shore of the lake; the colony was located on two ledges on a rock cliff at the southern edge of a large outcrop. The flat ledges were each 2 x 9 m. The water level had been lowered by a beaver dam on the feeder river several years previously, leaving the ledges about 15m above the water level. The site did not appear to have been disturbed by humans.

Pinawa Channel. On a rectangular outcrop (25 x 10 m), the long side forming the north shore of a small channel northwest of the diversion dams; the cacti were located on the upper slope and on the lower third which was a flat shelf sloping abruptly and steeply (1:3) to a maximum of five m above water level to the west and north. The water level in the channel was reduced by approximately 4m as a result of damming in the 1930s. The upper part of the rock outcrop on which the cacti were found previously formed part of the shore of the channel. The shoreline rock was broken and densely colonized by shrubs (especially Salix species). The flat surface above the outcrop had dense stands of Populus tremuloides, Quercus macrocarpa, and Corylus cornuta. Cacti were also found on a higher outcrop to the east which now is surrounded by forest.

MacArthur Falls. Cacti were located on a flat outcrop (30 x 9 m), 20 m from the north shore of a small island on the Winnipeg River, located approximately 1km upstream from a hydroelectric dam. The site was surrounded by Carex scoparius, Spiraea alba, and patches of Populus tremuloides. In the 1950s, damming raised the water level by 6m, leaving this rocky hilltop isolated as an island. Remains of a gravel highway, now colonized by trees, were visible on the island.

Bird River. Cacti were located on an outcrop (20 x 6 m) on the north shore of Bird River, 6km east of its mouth. The upper third of the rock (3 x 5 m) was almost flat. The mid-third consisted of a series of steps and steep slopes below which a very steep (1:1.3), smooth slope extended to the water. The outcrop was bounded on the west by unidentified grasses, on the north and east by Abies balsamea, Betula papyrifera, Populus tremuloides, and Corylus cornuta. No signs of human disturbance were observed during the study, however remains of an old campfire (colonized by mosses and Opuntia fragilis) and a canoe portage were present.

Bissett. An outcrop on the south shore of a large island near the north shore of Rice Lake; the cacti were located on the lower 15m of the outcrop where the rock sloped steeply (1:4) up from the waterline. The outcrop then sloped more gradually (1:6) to the top of the island. The outcrop was bounded by open stands of Pinus banksiana, Populus tremuloides, and Betula papyrifera.

The water level of Rice Lake was artificially raised for a short time between 1910 and 1930, then lowered to its original level. Since the 1960s there has been some disturbance of the site by cottage owners.

Climate

The temperature profile of the Bird River valley (Fig. 2.3) indicated that the north-facing slope was generally cooler than the south-facing. Comparison with the vegetation profile (Fig. 2.4) showed that the variation at points (1) and (4) occurred where openings in the forest received full sun and no wind. Temperatures were higher on outcrops (points 1, 7-9) than in the forest (points 2, 3, 5, 6, 11, and 12). Temperature differences were not tested due to small sample size.

Soils

Soil characteristics were extremely variable, especially in conductivity (Table 2.2). All soils were acidic and organic, with low bulk density. Outcrop soils had a higher organic content, lower pH, and lower phosphorous, potassium, and sulfate contents than forest soils ($P < 0.05$). Available nitrate was not compared, as it was probably altered by freezing (c.f. Seifert 1964).

Vegetation

Ten of the 153 species were common, i.e. present at six or seven sites (Appendix 2.3), including *Hedwigia ciliata*, *Opuntia fragilis*, *Prunus virginiana*, *Populus tremuloides*, and *Juniperus communis*. Twenty-two species, mostly angiosperms, were rare, i.e. found in quadrats at one site. Many were common nearby, e.g. *Corydalis sempervirens*, but others appeared to be restricted to single sites, e.g. *Grimmia unicolor*, *Polygonum douglasii*, *Prunus pumila*, and *Juniperus horizontalis*. A range of 14 to 32 species per site was encountered.

Figure 2.3: Temperature profile of Bird River valley.
(A) Location of thermometers on profile of valley,
Thermometers 1, and 7-10 = outcrop.
2-6 and 11-12 = forest.
(B) daily maximum temperatures, and
(C) daily minimum temperatures.
Day 1-3 = May 27-29, 1982.

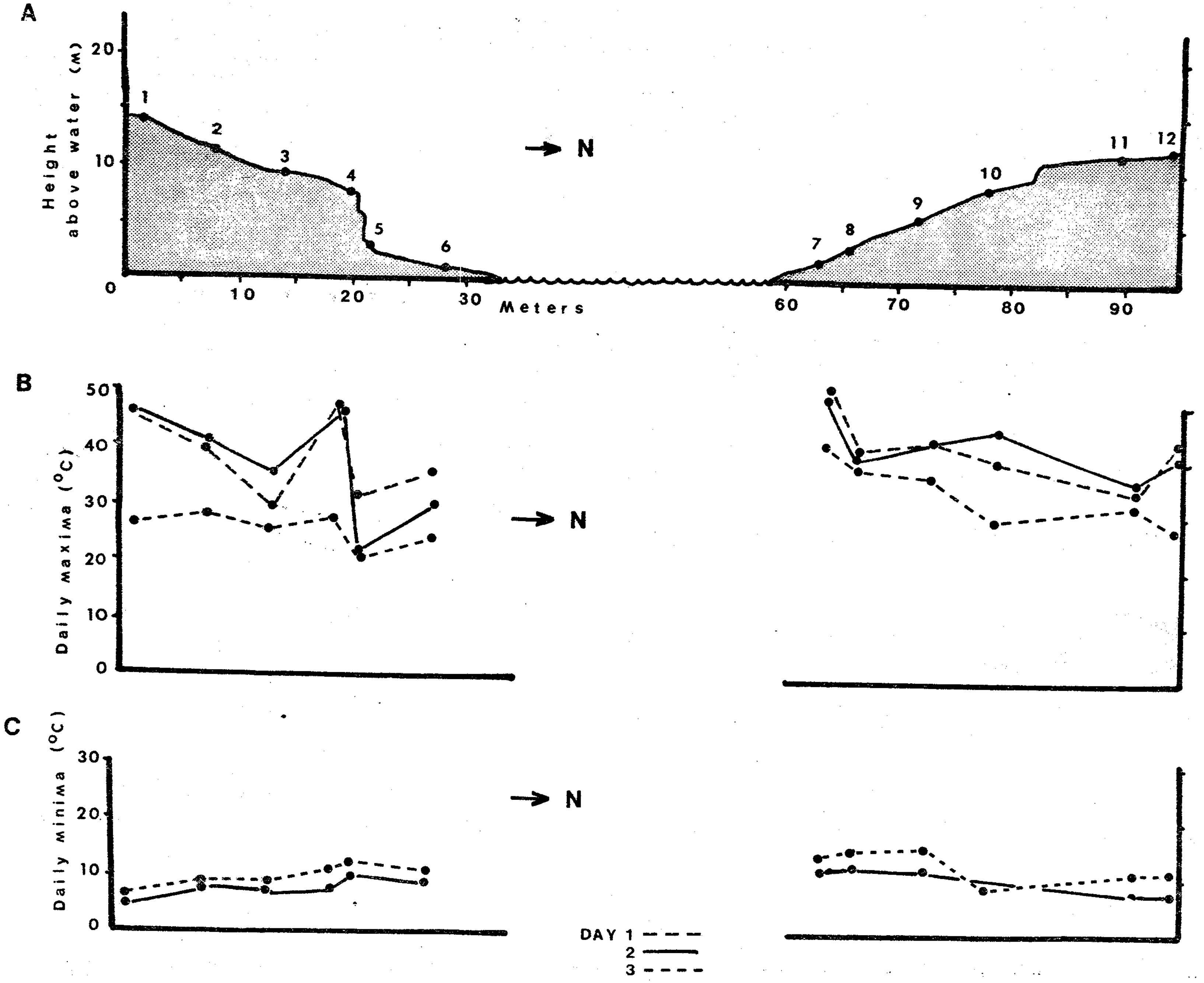

A
Height above water (M)
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
→ N
10
20
30
Meters
60
70
80
90
B
Daily maxima (°C)
50
40
30
20
10
0
→ N
C
Daily minima (°C)
30
20
10
0
→ N
DAY 1
2
3

Figure 2.4: Profile through Bird River valley at cactus site, showing vegetation zones and species assemblages.

A. Outcrop

Ribes glandulosum
Vaccinium myrtilloides
Prunus pensylvanica
Potentilla tridentata
Pleurozium schreberi
Cladina spp.

B. Forest

Picea mariana
Abies balsamea
Betula papyrifera
Vaccinium myrtilloides
Linnaea borealis
Maianthemum canadense
Polypodium virginianum

C. Forest

Abies balsamaea
Pinus banksiana
Amelanchier alnifolia
Juniperus communis
Vaccinium myrtilloides
Pleurozium schreberi

D. Clearing

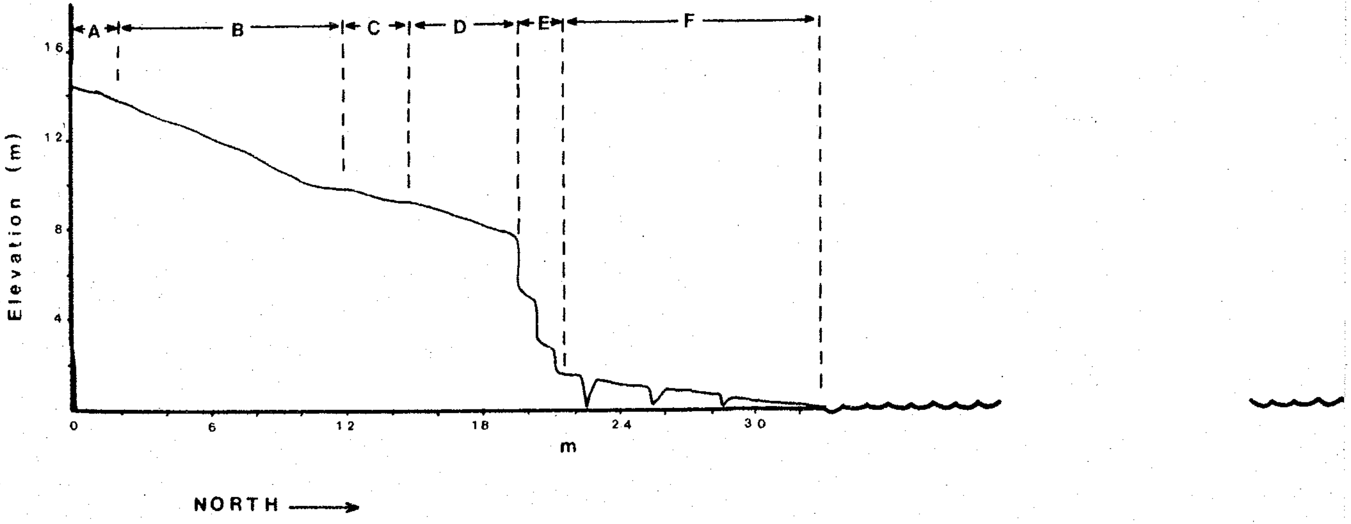
Vaccinium myrtilloides
Arctostaphylos uva-ursi
Cladina spp.
scattered *Picea mariana*
and *Pinus banksiana*

E. Cliff base

Abies balsamea
Viburnum sp.
Polypodium virginianum
Dryopteris disjuncta
Thuidium abietinum
Pleurozium schreberi
Polytrichum juniperinum

F. Boulders above water

Abies balsamea (seedling)
Viburnum sp.
Salix sp.
Alnus sp.
Rubus idaeus
Ribes glandulosum
Aralia nudicaulis
Fragaria virginianum
Polypodium virginianum
Pleurozium schreberi



fragilis

apocarpa

a ciliata

ruralis

e lichens

emorosa

ia parviflora

ga virginiensis

ier alnifolia

icarpos occidentalis

oreale

ergia sp.

nksiana (one tree)

p.

I. Forest

Abies balsamaea

Picea glauca

Populus tremuloides

Amelanchier alnifolia

Cladonia spp.

deep litter layer

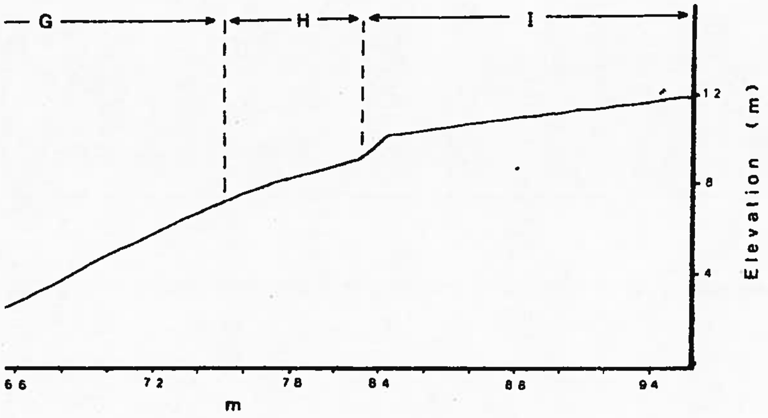


Table 2.2: Comparison of soil characteristics at seven outcrop and six forest sites using a Student's t-test. (Sokal and Rohlf 1969). * = significant difference between forest and outcrop at $P < 0.05$. () indicate forest soils.

Site		Soil Characteristics							
						Macronutrients (kg/ha)			
		pH	Conductivity (mmhos/cm)	% Organic matter	Bulk density (g/ml)	Available Nitrate	Available Phosphorous	Available Potassium	Available Sulfate
Falcon	2 (2)	5.05 (5.2)	0.25 (0.20)	62.1 (17.5)	0.27 (0.64)	9.6 (1.4)	9.8 (62.8)	102.9 (441.6)	2.6 (8.9)
Big Whiteshell	2 (2)	4.15 (5.1)	0.10 (0.20)	39.4 (41.2)	0.40 (0.39)	6.5 (36.0)	7.9 (25.9)	79.9 (224.1)	1.5 (6.6)
Betula	2 (0)	4.8 ---	0.05 ---	38.7 ---	0.40 ---	2.3 ---	10.0 ---	75.8 ---	1.9 ---
Pinawa	3 (3)	5.9 (6.0)	0.25 (0.23)	47 0 (30.9)	0.35 (0.47)	8.9 (3.1)	8.8 (14.2)	283.0 (461.5)	4.7 (10.1)
Bird River	2 (2)	5.00 (6.4)	0.10 (0.25)	53.4 (14.7)	0.31 (0.69)	10.3 (2.0)	6.7 (18.0)	56.8 (363.6)	2.1 (12.7)
MacArthur	1 (1)	4.4 (4.8)	0.20 (0.10)	32.4 (64.5)	0.46 (0.25)	9.3 (0.8)	7.8 (9.7)	60.2 (113.5)	11.8 (5.0)
Bissett	2 (2)	4.4 (4.5)	0.15 (0.15)	42.0 (40.7)	0.38 (0.39)	11.1 (1.1)	5.5 (82.7)	57.0 (254.7)	1.0 (15.6)
Mean ± 1 s	14 (12)	4.8 ± .6 (5.4 ± 0.8) *	0.15 ± .09 (0.20 ± 0.06)	46.7 ± 12.5 (32.1 ± 21.6) *	0.37 ± .06 (0.47 ± 0.17)	8.3 ± 3.0 (7.4 ± 14.0)	8.1 ± 1.6 (35.6 ± 3.0) *	102.2 ± 81.4 (309.8 ± 135.8) *	3.7 ± 3.8 (9.8 ± 3.9 *

The mean number of species per quadrat was consistent, but mean number of species per m^2 decreased with increased quadrat size (Fig. 2.5).

Life-form spectra (sensu Raunkiaer 1937, Appendix 2.2) of the outcrop and forest habitats (Fig. 2.6) showed a predominance of phanerophytes. Most of the tree species found on outcrops were common to the forest and represented by solitary individuals. Outcrops contained more thallophytes, therophytes and chamaephytes than the forest, but fewer hemicryptophytes and geophytes.

A few species, mostly shrubs, were common to both outcrop and forest habitats (Table 2.3). Half the species restricted to forest samples were shrubs (Table 2.4). Species confined to outcrops were herbs and low shrubs (hemicryptophytes and chamaephytes, respectively), with some moss species (thallophytes, Table 2.5).

On the outcrops, sample placement determined that *Opuntia fragilis* dominated the $0.09m^2$ quadrats, but its cover decreased in larger quadrats (Fig. 2.7a). Bare rock and tree/shrub cover increased with quadrat size, while total vegetation cover decreased (Fig. 2.7b-e).

In the forest, cover values of the vegetation components (Fig. 2.7) were stable. Moss/lichen and bare rock cover were lower than on outcrops, presumably due to the continuous litter layer. Tree/shrub and total vegetation covers were higher than on outcrops. Total cover over 100% (Fig. 2.7d) was attributed to the closed canopy and multiple strata.

Figure 2.5: Mean number of species per m^2 and per quadrat versus quadrat size in outcrop and forest habitats.

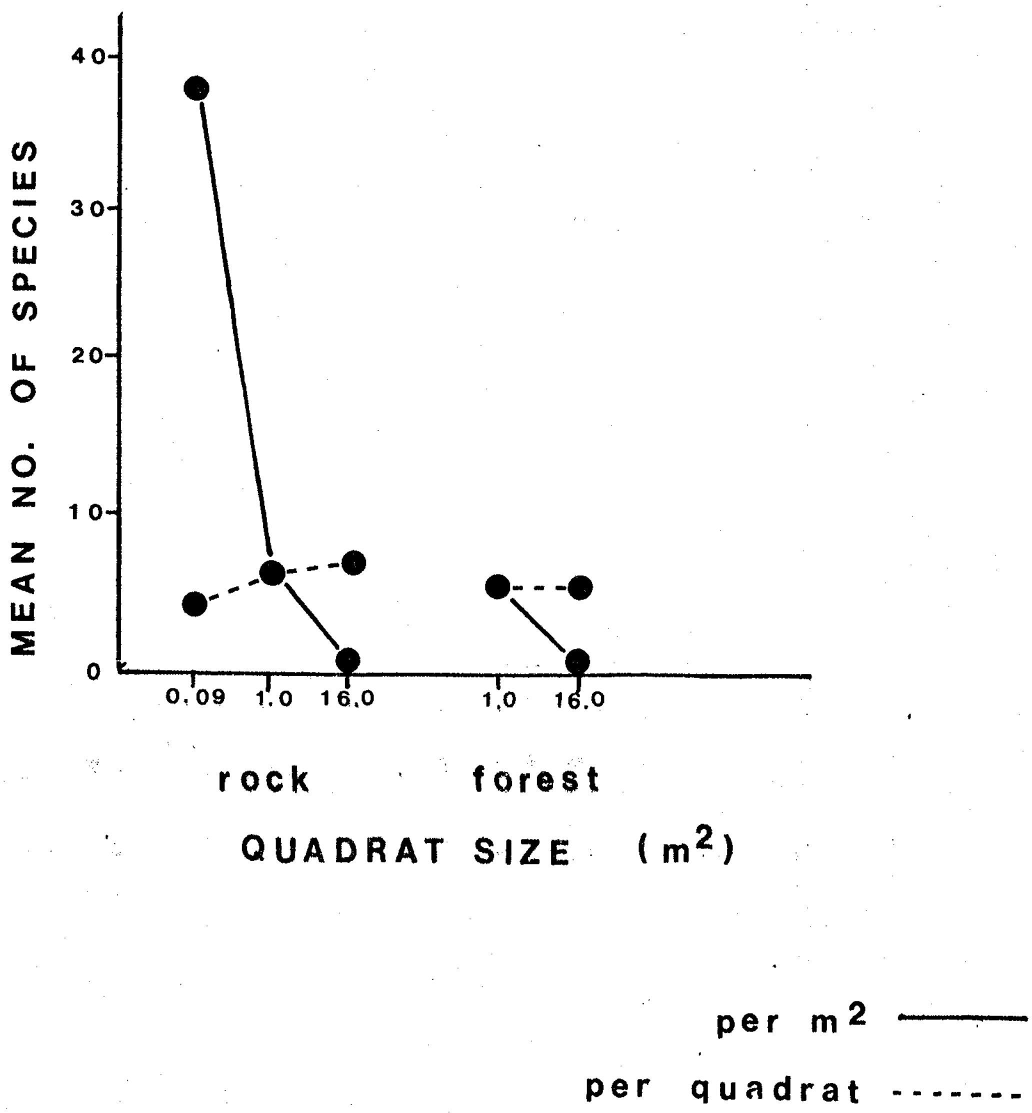

MEAN NO. OF SPECIES
40
30
20
10
0
0.09
1.0
16.0
1.0
16.0
rock
forest
QUADRAT SIZE (m2)
per m2 ———
per quadrat -------

Figure 2.6: Raunkiaer's lifeform spectrum (see Appendix 2.2) for outcrops and forest quadrats, showing species common to both habitats as well as those restricted to one habitat.

Th - Thallo-hemicryptophytes,
Tc - Thallo-cryptophytes,
T - Therophytes,
G - Geophytes,
H - Hemicryptophytes,
Ch - Chamaephytes, and
Ph - Phanerophytes.

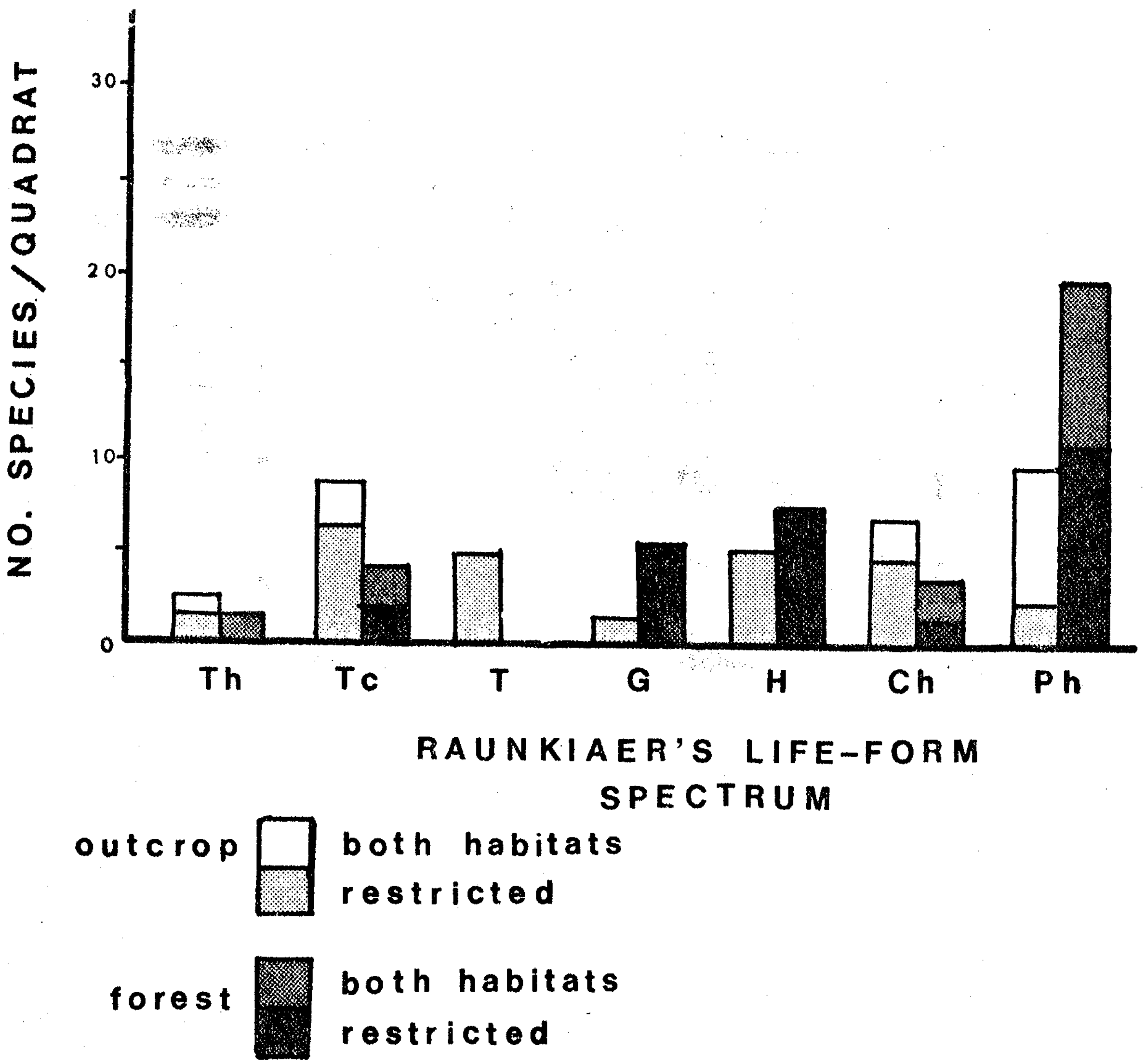

NO. SPECIES/QUADRAT
30
20
10
0
Th
Tc
T
G
H
Ch
Ph
RAUNKIAER'S LIFE-FORM SPECTRUM
outcrop
both habitats
restricted
forest
both habitats
restricted

Figure 2.7: Percent cover of vegetation groups and bare rock in various quadrat sizes.

(A) 0.09m^2
(B) 1.0m^2
(C) 16.0m^2

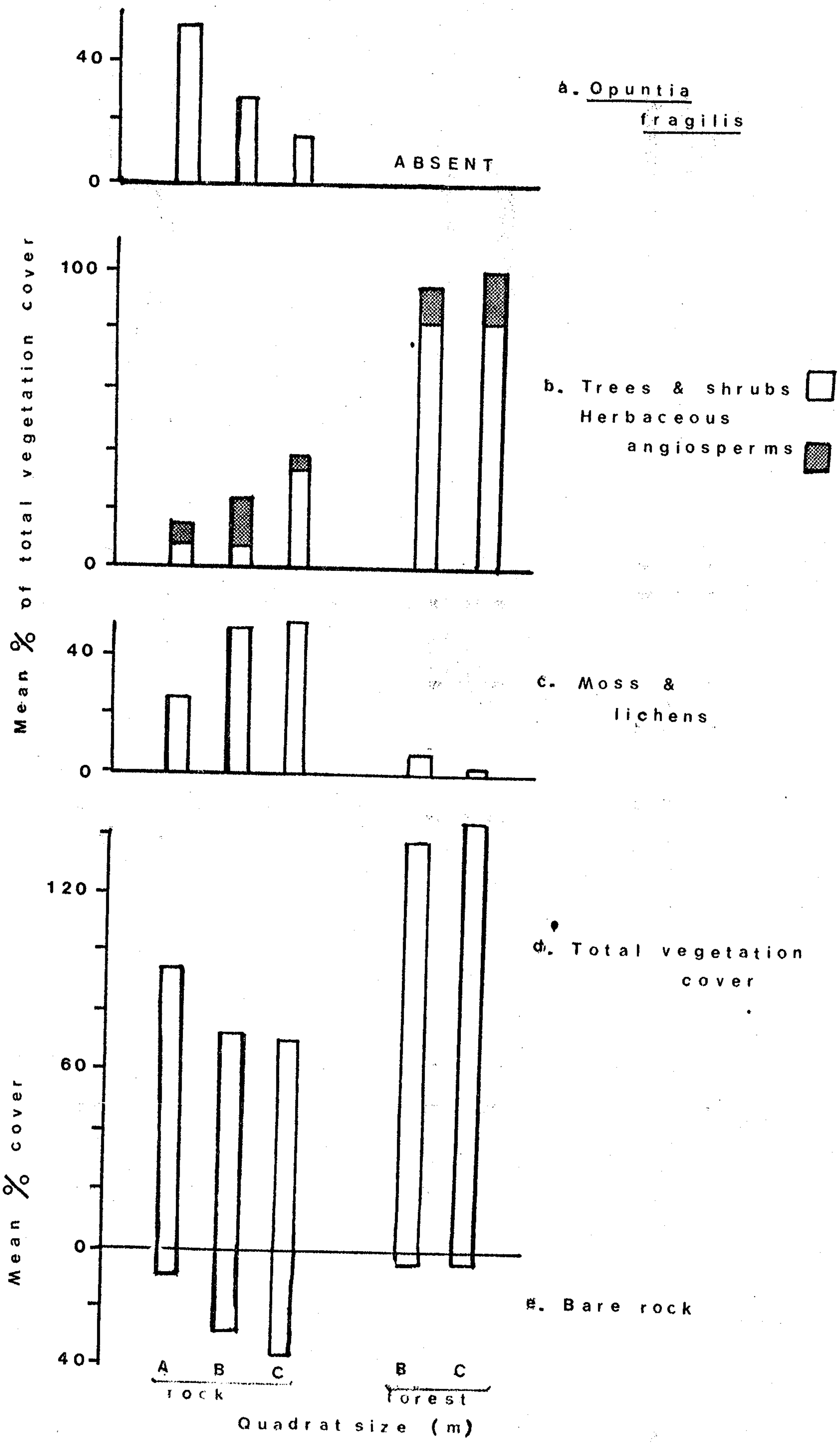

a. Opuntia fragilis
ABSENT
40
0
b. Trees & shrubs ☐
Herbaceous angiosperms ▨
100
0
c. Moss & lichens
40
0
Mean % of total vegetation cover
d. Total vegetation cover
e. Bare rock
120
60
0
40
Mean % cover
A
B
C
rock
B
C
forest
Quadrat size (m)

Table 2.3: Species common to both forest and rock outcrop quadrats from seven sites, including their classification by life-form (fide Scoggan 1978 - see Appendix 2.1 for definitions). *Nomenclature of mosses Crum (1976).

Species	Life-form
foliose lichens	Th
fruticose lichens	Tc
Polytrichum juniperinum Hedw.*	Tc
Populus tremuloides Michx.	Ph
Quercus macrocarpa Michx.	Ph
Ribes oxyacanthoides L.	Ch
Rosa spp.	Ch
Rubus idaeus L.	Ch
Prunus virginiana L.	Ph
P. pensylvanica L.	Ph
Amelanchier spp.	Ph
Viburnum rafinesquianum Schultes	Ph
Symphoricarpos albus (L.) Blake	Ph

Table 2.4: Species (fide Scoggan 1978) restricted to forest sample quadrats at seven sites. *Nomenclature of moss fide Crum (1976).

Species	Life-form
Pleurozium schreberi (Brid.) Mitt.*	Tc
Picea glauca (Moench) Voss	Ph
Abies balsamea (L.) Mill.	Ph
Clintonia borealis (Ait.) Raf.	G
Maianthemum canadense Desf.	G
Smilacina stellata (L.) Desf.	G
Corylus americana Walt.	Ph
C. cornuta Marsh.	Ph
Betula papyrifera Marsh.	Ph
Polygonum cilinode Michx.	H
Anemone quinquefolia L. var. *interior* Fern.	G
Fragaria virginiana Duchesne	H
Rubus pubescens Raf.	H
Acer spicatum Lam.	Ph
Aralia nudicaulis L.	Ch
Cornus canadensis L.	H
Pyrola asarifolia Michx.	H
Vaccinium spp.	Ph
Fraxinus nigra Marsh.	Ph
Apocynum androsaemifolium L.	G
Galium labradoricum Wieg.	H
G. boreale L.	H
Lonicera dioica L. var. *glaucescens* (Rydb.) Butters	Ph
L. oblongifolia (Goldie) Hook.	Ph
Diervilla lonicera Mill.	Ph

Table 2.5: Species (fide Scoggan 1978) restricted to rock outcrop sample quadrats at seven sites. *Nomenclature of mosses fide Crum (1976).

Species	Life-form
grey crustose lichens	Th
Tortula ruralis (Hedw.) Gartn., Meyer & Scherb.*	Tc
Grimmia apocarpa Hedw.*	Tc
Hedwigia ciliata (Hedw.) P. Beauv.*	Tc
Bryum pseudotriquetrum (Hedw.) Gartn., Meyer & Scherb.*	Tc
Thuidium abietinum (Hedw.) BSG*	Tc
Polytrichum piliferum Hedw.*	Tc
Juniperus communis L.	Ch
J. horizontalis Moench	Ch
Panicum capillare L.	T
Agrostis sp.	Hs
Allium stellatum Fraser	Gb
Betula glandulosa Michx. var. glandulifera (Regel) Gl.	N
Polygonum convolvulus L.	T
Silene noctiflora L.	T
Corydalis sempervirens (L.) Pers.	Hs
Prunus pumila L.	Ch
Geranium bicknellii Britt.	T
Rhus glabra L.	N
Opuntia fragilis (Nutt.) Haw.	Ch
Campanula rotundifolia L.	Hsr
Achillea millefolium L.	Hsr

The following species were observed to be restricted to outcrops, but did not occur in the sample quadrats (see Appendix 2.3):

Andropogon gerardi Vit.
Heuchera richardsonii R.Br.
Saxifraga virginiensis Michx.
Grimmia unicolor Hook. ex. Grev.*
Agropyron trachycaulon (Link.) Malte

Description of Cactus Colonies

The cactus colonies (Table 2.6) ranged from three discrete clumps with a total of 354 pads (MacArthur Falls) to over 50 clumps with a total of about 8,000 pads (Big Whiteshell). Colony size was not correlated with any soil variable. They were located 0.9-15m vertically, and 10.5-32.0m horizontally from water level.

In 1980, field-collected pads from Bissett and Betula Lake were smallest, those from Bird River, MacArthur Falls, and Big Whiteshell largest (Table 2.7). Mean values for pad weight, length, and width did not differ significantly between Betula Lake and Bissett ($P > 0.05$). Bird River and MacArthur Falls differed only in width. After one year under uniform laboratory conditions (Table 2.8), the field-collected pads from Bissett and Betula Lake remained smallest, and those from MacArthur Falls and Bird River remained similar ($P > 0.05$). Pads from Big Whiteshell had become smaller. There were fewer significant differences in the second year means than in the first.

"Second generation pads" (new pads produced by field-collected pads in the laboratory) showed even fewer differences among sites (Table 2.9). Mean lengths and dry weights (biomass) were not statistically different among the sites ($P > 0.05$). Bissett and Betula Lake pads were no longer consistently smallest. The width of Big Whiteshell pads remained greatest ($P < 0.05$). The distinctive groupings of sites by pad length and depth in 1980 were absent in the progeny pads.

Pad characters were not significantly correlated with mean soil values (Appendix 2.5).

Table 2.6: Characteristics and locations of cactus colonies at seven sites.

Site	# clumps of cacti on outcrop	approx. # pads on outcrop	maximum distance from water (m)	
			horizontal	vertical
Falcon	10 - 15	5,000	10.5	0.9
Big Whiteshell	50 +	8,000	20.0	3.0
Betula	10 - 15	1,000 +	30.0	15.0
Pinawa	16	1,300 +	18.5	2.5
Bird River	31	3,000 +	20.0	7.0
MacArthur Falls	3	354	22.0	2.0
Bissett	20	4,000	30.0	8.0

Table 2.7: Means of characters of original pads in 1980. Sites joined by bars do not differ significantly (P > 0.05) using analysis of variance and Student's t-tests. (MacA = MacArthur Falls, Big W = Big Whiteshell Lake)

Pad Character	Means (arranged in order of magnitude)						
Fresh Weight (g)	Site:	Bissett	Betula	Falcon	Bird	MacA	Big W
	Mean:	1.36	1.50	2.10	2.68	2.99	3.03
Length (mm)	Site:	Bissett	Betula	Falcon	Big W	MacA	Bird
	Mean:	20.25	22.65	28.10	31.80	31.80	32.90
Width (mm)	Site:	Betula	Bissett	Falcon	Bird	MacA	Big W
	Mean:	12.80	13.75	14.55	15.30	16.60	18.95
Depth (mm)	Site:	Bissett	Betula	Big W	Falcon	Bird	MacA
	Mean:	8.60	9.40	9.50	9.85	10.65	10.90

Table 2.8: Means of characters of original pads after one year under uniform conditions. Sites connected by bars do not differ significantly (P > 0.05) using analysis of variance and Student's t-test. (MacA = MacArthur Falls, Big W = Big Whiteshell Lake)

Pad Character		Means (arranged in order of magnitude)					
Fresh Weight (g)	Site:	Bissett	Betula	Falcon	MacA	Bird	Big W
	Mean:	0.98	1.43	2.00	2.44	2.45	2.59
Length (mm)	Site:	Bissett	Betula	Big W	Falcon	MacA	Bird
	Mean:	14.4	17.10	21.75	22.29	22.70	27.20
Width (mm)	Site	Betula	Bissett	Falcon	MacA	Bird	Big W
	Mean:	10.60	10.90	12.43	13.30	14.05	14.55
Depth (mm)	Site	Bissett	Betula	Big W	Falcon	MacA	Bird
	Mean:	5.90	7.00	7.10	8.38	8.70	8.75
Shoot biomass (g)	Site:	Bissett	Betula	Falcon	Bird	MacA	Big W
	Mean:	.21	.29	.40	.44	.47	.48.
Root biomass (g)	Site:	Betula	Bissett	Falcon	Big W	MacA	Bird
	Mean:	.047	.050	.067	.079	.080	.080

Table 2.9: Means of characters of second generation pads, 1981. Sites joined by bars do not differ significantly ($P > 0.05$) using analysis of variance and Student's t-test. (MacA = MacArthur Falls, Big W = Big Whiteshell Lake)

Pad Character	Means (arranged in order of magnitude)						
Fresh weight (g)	Site:	Betula	Bird	Falcon	Bissett	MacA	Big W
	Mean:	0.74	0.74	0.81	0.84	1.02	1.05
Length (mm)	Site:	Bird	Betula	Big W	Falcon	Bissett	MacA
	Mean:	17.73	20.55	22.50	22.52	23.34	26.31
Width (mm)	Site:	Bissett	MacA	Falcon	Betula	Bird	Big W
	Mean:	6.05	7.42	7.64	7.80	7.91	10.23
Depth (mm)	Site:	Bissett	Falcon	Big W	MacA	Betula	Bird
	Mean:	4.82	5.96	6.15	6.62	6.80	6.91
Biomass (g)	Site:	Bird	Betula	Bissett	MacA	Falcon	Big W
	Mean:	0.136	0.144	0.145	0.182	0.187	0.188

Discussion

Distribution and Abundance

A series of thirty-six geographically and ecologically isolated colonies of Opuntia fragilis extends across southeastern Manitoba (49°37'N 95°12'W to 51°02'N 95°41'W) in the watersheds of the Winnipeg, Wanipigow/Manigotagan, and Lake of the Woods river systems. An unverified colony was reported at Norway House. On the basis of numbers, I feel that White and Johnson (1980) are justified in excluding this species from the rare and endangered species in Manitoba.

Most of the colonies examined had more than 1000 pads each, with the largest colony on an island in Big Whiteshell Lake (ca. 8000 pads). Colony dimensions, pad number, and the number of colonies per outcrop were not correlated with soil characteristics. They are likely related to the time since original colonization and to frequency of disturbance at that site. The proportion of new pads per colony appears to increase at about the same rate at all sites. Human disturbance, which results in the establishment of new colonies, may preclude enlargement of colonies at the Pinawa, Bird River, and Falcon Lake sites.

Natural disturbance by flood, violent rainfall, or animals may also disrupt colonies and result in the formation of new ones.

Habitat

The typical habitat of Opuntia fragilis in the Boreal Forest Region of southeastern Manitoba can be summarized as follows:

sloping, south-facing outcrops on islands or shores of waterways; approximately ? 4m above water (except where water level has been manipulated); in mats of moss, often in shallow cracks or depressions. Restriction to waterways suggests that the species has been eliminated from inland sites, and/or that dispersal is primarily by hydrochory. Restriction to outcrops suggests adaptation to stress-tolerance. Although the outcrops in this region share the general climate (i.e. humid continental), glacial history, and physiography of the surrounding forest, they differ from forest in absence of glacial deposits, microclimate, and vegetation cover. The discrete outcrops resemble xeric islands in an otherwise mesic environment.

Outcrop soils are shallow, confined to cracks or depressions, and are composed of organic debris with a small mineral fraction derived from granitic bedrock. The outcrop soils are also more acidic and poorly drained, and less fertile, than the till-derived forest soils. They are readily saturated by melt- or rain-water, but their shallowness results in rapid drying, hence they fluctuate between drought and innundation.

The virtual absence of an insulating layer on outcrops results in wide temperature fluctuations (c.f. Rejmanek 1971). In late May, the Bird River outcrop surface was as much as 15°C warmer than surrounding areas. Outcrops are often snow-free before the adjacent forest, and support winter annuals. At Bird River, flowers on a branch of Prunus virginiana resting on the rock surface reached anthesis several days before those on upright branches.

There is presumably an annual rain of propagules from mesophytic boreal species on the outcrop, but the xeric outcrop habitat limits them to mesic micro-habitats, e.g. deep sheltered crevices. South-facing outcrops are ecologically similar to prairie habitats, especially in fluctuating moisture and temperature regimes that result in summer drought. Many of the outcrop species are also common in grasslands (Löve 1959), and exhibit adaptations to moisture and temperature stress (Grime 1979): succulence, sclerophyllous or summer-deciduous leaves, seasonally restricted flower production, seasonal vegetative growth, absence or irregularity of seed production, long life-span, seasonal germination, and regeneration by dust propagules (e.g. spores). Opuntia fragilis exhibits all but the last two adaptations.

Phenotypic Variation

The phenotypic variation in field-collected pads was not strongly related to any of the soil properties measured. Pad length appeared to vary with light intensity which, in turn, was related to the slope, aspect, and exposure of individual outcrops. Fresh weight was directly related to water content of succulent tissue, which varied with season, site physiography, and soil water-holding characteristics. Pad characters could not be used to differentiate colonies.

Conclusions

Colonies of Opuntia fragilis are scattered throughout the Boreal Forest Region of southeastern Manitoba. They are confined to waterways, where they occur on south-facing rock outcrops, 3-4 m above water level. This habitat was characterized by high light intensity and temperature, wide moisture fluctuation, and low soil pH and nutrient content. Pad morphology was not correlated with soil variables, but etiolation of pads under artificial conditions suggested a requirement for high light intensity.

The seven colonies under study contained over 1000 pads each. New pads, which are produced annually, provided a source of propagules for further spread.

Appendix 2.1: Locations of posters requesting reports of *Opuntia fragilis* in Manitoba.

1. Lyleton
2. Waskada
3. Pierson
4. Tilston
5. Deloraine
6. Melita
7. Killarney
8. Cartwright
9. Snowflake
10. Darlington
11. Morden
12. Winkler
13. Altona
14. Carman
15. Reston
16 Elkhorn
17. Rivers
18. Miniota
19. Roblin
20. Swan River
21. Bowsman
22. Pelican Rapids
23. McCreary
24. Erickson
25. Minnedosa
26. Neepawa
27. Glenboro
28. Alexander
29. Gladstone
30. Crane River
31. Ebb & Flow
32. Waterhen
33. Moose Lake
34. Pukatawagan
35. Nelson House
36. God's Lake
37. Island Lake
38. St. Theresa Point
39. Oxford House
40. Norway House
41. Split Lake
42. Snow Lake
43. Herb Lake
44. Grand Rapids
45. Flin Flon
46. Wanless
47. Pine River
48. Wekusko
49. Thicket Portage
50. Jenpeg
51. Wabowden
52. Pigeon River
53. Berens River
54. Amaranth
55. Easterville
56. Blood Vein
58. Highrock
59. Fort Alexander
60. Great Falls
61. Bissett
62. Pointe du Bois
63. Wanipigow
64. Manigotagan
65. Falcon Lake
66. Sprague
67. Gillam
68. Lac du Bonnet
69. Pinawa
70. Pine Falls
71. Thompson
72. Little Grand Rapids
73. The Pas
74. Libau
75. Rennie
76. Whitemouth
77. Grandview

Appendix 2.2: Life-form classification of plants.
(modified from Scoggan 1978).

Abbreviation	Life-form
	Phanerophytes (Ph) - trees
Ms	Mesophanerophytes, 8-30 m.
Mc	Microphanerophytes, 2-8 m.
N	Nanophanerophytes, 25 cm to 2 m.
	Chamaephytes (Ch) - shrubs
Ch	(Shrubs)
	Hemicryptophytes (H) - perennating organs at ground surface
Hp	Proto Hemicryptophytes, no runners
Hpr	Proto Hemicryptophytes, with runners
Hs	Hemicryptophytes, semi-rosette, no runners
Hsr	Hemicryptophytes, semi-rosette, with runners
Hr	Hemicryptophytes, rosette, no runners
Hrr	Hemicryptophytes, rosette, with runners
	Cryptophytes (Cr) - subterranean perennating organs
Grh	Rhizome geophyte
Gst	Stem-tuber geophyte
Grt	Root-tuber geophyte
Gr	Root geophyte
Gb	Bulb-tuber geophyte
Hel	Helophyte, perennating buds submersed or in mud.
T	Therophytes (T) - annuals
	Thallophytes - non-vascular low-growing plants
Th	Thallo-hemicryptopyte
Tc	Thallo-cryptophyte

Appendix 2.3: Species list for quadrat study at seven sites, with life-form (Scoggan 1978). R = on rock outcrop; F = forest habitat. Bryophytes fide Crum (1976), verified by R.R. Ireland. Lichens verified by P. Wong.

		Bird	Big Whiteshell	Bissett	Betula	MacArthur	Pinawa	Falcon
	1. LICHENS							
Th	CRUSTOSE	R	R	R	R	R	R	R
Th	FOLIOSE	RF	R	RF	R	R	R	R
Tc	FRUTICOSE	R	R	RF	R	R		R
	2. BRYOPHYTES							
	POTTIACEAE							
Tc	*Tortula ruralis* (Hedw.) Gtrtn., Meyer & Scherb.	R	R				R	
	GRIMMIACEAE							
Tc	*Grimmia apocarpa* Hedw.					R		
	HEDWIGIACEAE							
Tc	*Hedwigia ciliata* (Hedw.) P.-Beauv.		R					
	BRYACEAE							
Tc	*Bryum pseudotriquetrum* (Hedw.) Gtrtn., Meyer & Scherb.		R					
	LESKEACEAE							
Tc	*Thuidium abietinum* (Hedw.) BSG	R				R		
	BRACHYTHECIACEAE							
Tc	*Pleurozium schreberi* (Brid.) Mitt.			F				
	POLYTRICHACEAE							
Tc	*Polytrichum juniperinum* Hedw.			RF				R
Tc	*P. piliferum* Hedw. in.			R	R			

		Bird	Big Whiteshell	Bissett	Betula	MacArthur	Pinawa	Falcon
	4. CONIFERS							
	PINACEAE							
Ms	*Picea glauca* (Moench) Voss	F						
Ms	*Abies balsamea* (L.) Mill.	F		F		F		F
Ch	*Juniperus communis* L.			R	R	R		
Ch	*J. horizontalis* Moench			R				
	5. ANGIOSPERMS							
	GRAMINEAE							
T	*Panicum capillare* L.				R			
Hs	*Agrostis* sp.					R		
	CYPERACEAE							
Hs	*Carex scoparia* Schk.					F	F	R
	LILIACEAE							
Grh	*Clintonia borealis* (Ait.) Raf.							F
Gb	*Allium stellatum* Fraser				R			
Grh	*Maianthemum canadense* Desf.	F					F	F
Grh	*Smilacina stellata* (L.) Desf.							F
	SALICACEAE							
M	*Salix* spp.			F		F		
Ms	*Populus tremuloides* Michx.	F	F	F	F		F	RF
	BETULACEAE							
Mc	*Corylus americana* Walt.						F	
Mc	*C. cornuta* Marsh.	F						F
N	*Betula glandulosa* Michx. var. *glandulifera* (Regel) Gl.			R			R	
Ms	*B. papyrifera* Marsh.	F		F				F
	FAGACEAE							
Mg	*Quercus macrocarpa* Michx.						RF	

		Bird	Big Whiteshell	Bissett	Betula	MacArthur	Pinawa	Falcon
	POLYGONACEAE							
Hp	*Polygonum cilinode* Michx.		F					
T	*P. convolvulus* L.		R	R				
	CHENOPODIACEAE							
T	*Chenopodium hybridum* L. var. *gigantospermum* (Aellen) Rouleau		F					
	CARYOPHYLLACEAE							
T	*Silene noctiflora* L.							R
	RANUNCULACEAE							
Grh	*Anemone quinquefolia* L. var. *interior* Fern.						F	
	FUMARIACEAE							
Hs	*Corydalis sempervirens* (L.) Pers.	R						
	SAXIFRAGACEAE							
N	*R. oxyacanthoides* L.	R		R	R	RF	RF	R
	ROSACEAE							
N	*Spiraea alba* Du Roi			R	R	F		
N	*Rosa* spp.	F		R			R	R
Hrr	*Fragaria virginiana* Duchesne						F	
Hp	*Rubus idaeus* L.		F	R		F	RF	
Hpr	*R. pubescens* Raf.	F						
Mc	*Prunus virginiana* L.	F	F	R		F	RF	R
Ms	*P. pensylvanica* L.	F					R	R
Ch	*P. pumila* L.				R			
Mc	*Crataegus* spp.							
Mc	*Amelanchier* spp.	F		F			RF	R

		Bird	Big Whiteshell	Bissett	Betula	MacArthur	Pinawa	Falcon
	GERANIACEAE							
T	*Geranium bicknellii* Britt.	R						
	ANACARDIACEAE							
N	*Rhus glabra* L.	R			R		R	R
	ACERACEAE							
Mc	*Acer spicatum* Lam.	F						
	VITACEAE							
Ms	*Parthenocissus inserta* (Kerner) K. Fritsch		F					
	CACTACEAE							
Ch	*Opuntia fragilis* (Nutt.) Haw.	R	R	R	R	R	R	R
	ONAGRACEAE							
Hp	*Epilobium angustifolium* L.					F		
Hs	*Oenothera biennis* L.	R		R				
	ARALIACEAE							
Ch	*Aralia nudicaulis* L.							F
	CORNACEAE							
Hpr	*Cornus canadensis* L.							F
	PYROLACEAE							
Hrr	*Pyrola asarifolia* Michx.	F						F
	ERICACEAE							
N	*Vaccinium* spp.			F		F		
	OLEACEAE							
Ms	*Fraxinus nigra* Marsh.	F						
	APOCYNACEAE							
Grh	*Apocynum androsaemifolium* L.						F	F

		Bird	Big Whiteshell	Bissett	Betula	MacArthur	Pinawa	Falcon
	RUBIACEAE							
Hp	*Galium labradoricum* Wieg.	F					F	
Hpr	*G. boreale* L.							F
	CAPRIFOLIACEAE							
Mc	*Lonicera dioica* L. var. *glaucescens* (Rydb.) Butters						F	
N	*L. oblongifolia* (Goldie) Hook.	F					F	
N	*Viburnum rafinesquianum* Schultes	F					RF	R
N	*Diervilla lonicera* Mill.	F						F
N	*Symphoricarpos albus* (L.) Blake	F			R		RF	R
	CAMPANULACEAE							
Hsr	*Campanula rotundifolia* L.			R				R
	COMPOSITAE							
Hpr	*Solidago rigida* L.						F	
H	*Aster* spp.	F						
Hsr	*Achillea millefolium* L.							R
Hs	*Cirsium muticum* Michx.						F	
	Number of species encountered	32	14	24	14	17	28	30

Appendix 2.4: Reported locations of colonies of *Opuntia fragilis* in the Boreal Forest Region of southeastern Manitoba.
(* = specimens collected)

	SITE	LONGITUDE	LATITUDE
1.	* Indian Bay	49°37'N	95°12'W
2.	* Falcon Lake	49°43'N	95°15'W
3.	* Sailing Lake	49°57'N	95°18'W
4.	* Big Whiteshell Lake	50°06'N	95°20'W
5.	* Betula Lake	50°05'N	95°35'W
6.	* Otter Falls, Margaret Lake	50°14'N	95°46'W
7.	* Sylvia Lake	50°11'N	95°55'W
8.	* Pinawa	50°09'N	95°53'W
9.	* Bird River	50°25'N	95°41'W
10.	* MacArthur Falls, Winnipeg River	50°24'N	96°00'W
11.	* Rice Lake (Bissett)	51°02'N	95°41'W
12.	Mud Turtle Lake	49°55'N	95°34'W
13.	War Eagle Lake	49°57'N	95°35'W
14.	Drummie Lake (= Cactus L.)	49°59'N	95°15'W
15.	Jessica Lake	50°00'N	95°36'W
16.	White Lake	50°02'N	95°37'W
17.	Heart Lake	50°07'N	95°42'W
18.	Nutimik Lake	50°08'N	95°41'W
19.	Numao Lake	50°09'N	95°40'W
20.	Slave Falls, Winnipeg River	50°13'N	95°34'W
21.	Blind Bay, Winnipeg River	50°18'N	95°28'W
22.	Eaglenest Lake	50°23'N	95°14'W
23.	Bird Lake	50°28'N	95°20'W
24.	Slate Lake	50°44'N	95°12'W
25.	Pillow Falls, Manigotagan River	51°01'N	95°50'W
26.	Turtle Lake	49°59'N	95°47'W
27.	Quesnel (Caribou) Lake	49°55'N	95°39'W
28.	Lake Wanipigow	51°06'N	96°00'W
29.	Lake Winnipeg (islands off Manigotagan)	51°14'N	96°18'W
30.	Rice River	51°16'N	96°25'W
31.	Norway House	54°00'N	97°48'W

Appendix 2.5: Correlation matrix of pad characteristics with mean soil characteristics at six sites. Values are for first year field collected pads (combined with second year in brackets).

Soil	Pad				
	Fresh weight (g)	Length (mm)	Width (mm)	Depth (mm)	Volume (mm^3)
pH	-0.17 (-0.08)	0.02 (0.09)	-0.41 (-0.15)	0.18 (0.13)	-0.12 (-0.06)
conductivity (mmhos/cm)	0.09 (0.07)	0.10 (0.07)	0.05 (0.03)	0.14 (0.10)	0.08 (0.07)
available nitrate (kg/ha)	0.11 (0.07)	0.13 (0.11)	0.09 (0.07)	0.11 (0.07)	0.13 (0.10)
available phosphorous (kg/ha)	-0.03 (0.02)	0.02 (0.02)	-0.12 (-0.06)	0.08 (0.07)	-0.04 (-0.01)
available potassium (kg/ha)	-0.03 (0.01)	0.01 (0.01)	0.01 (-0.00)	-0.08 (0.00)	-0.05 (-0.02)
sulfate (kg/ha)	0.34 (0.24)	0.27 (0.16)	0.19 (0.09)	0.43 (0.20)	0.33 (0.26)
% organic matter	-0.09 (-0.03)	0.07 (0.10)	-0.17 (-0.04)	0.03 (0107)	-0.06 (-0.02)
bulk density (g/ml)	0.13 (0.06)	-0.03 (-0.08)	0.20 (0.05)	0.02 (-0.04)	0.10 (0.05)

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CHAPTER THREE

Factors Determining the Distribution of Opuntia fragilis in Southeastern Manitoba

ABSTRACT

The effects of propagule dispersal, establishment, and maintenance on the distribution of *Opuntia fragilis* (Nutt.) Haw. in southeastern Manitoba were tested at Bird River (50°25'N, 95°41'W) from May 1981 - October 1982. Because the cactus propagates vegetatively in this region, the propagules used were stem units (pads).

Mark and recapture, flotation experiments, and field observations indicated three potential dispersal mechanisms. In order of increasing risk to survival, they were:

1. geochory, which dispersed pads locally and introduced them into the river.
2. hydrochory, which dispersed pads over long distances, but restricted their spread to waterways.
3. epizoochory, which also functioned over long distances, given suitable vectors (e.g. humans).

Marked pads were planted in habitats to which they might be dispersed. After one year, establishment was significantly greater ($P < 0.05$) on south-facing outcrops than on north-facing or forest sites.

Censuses (1979 - 1982) of an established colony indicated that pad number was increasing by 30% per year. Approximately 6% of the pads were dispersed from the outcrop.

The original date of arrival in Manitoba is unknown, but three time periods may be hypothesized: 9000 - 7500 years BP, 7500 - 4000 BP, or 4000 - 0 BP. The present distribution of *O. fragilis* appears to be maintained by hydrochory and/or epizoochory along canoe routes. The cactus is both habitat and dispersal limited.

CHAPTER THREE

Factors Determining the Distribution of *Opuntia fragilis* in Southeastern Manitoba

Introduction

In the Boreal Forest Region of southeastern Manitoba, *Opuntia fragilis* is restricted to certain south-facing outcrops on waterways (Chapter II). This discontinuous distribution suggested that the cactus colonies were relics of past assemblages, recent colonizers, or restricted by dispersal and/or habitat. The aim of this study was to examine the influence of three factors in the determination of this distribution: propagule dispersal, establishment (i.e. rooting), and maintenance (i.e. growth and propagation). Propagules used in this study were stem segments (pads) because *O. fragilis* propagated entirely by vegetative means in the study region (Chapters I and II).

Methods and Materials

Pads used in the following experiments were collected in May 1981 from a colony on the Bird River (50°25'N, 95°41'W) in southeastern Manitoba. Experiments (1b), (2), and (3) were carried out at this site.

1. *Dispersal*

(a) *Hydrochory*. Pad flotation was tested using 40 one-year-old pads. Each was placed in a 500ml Ehrlenmeyer flask containing approximately four cm of distilled water. Twenty flasks were agitated continuously at 150 rpm while 20 were not agitated. The number of floating pads was recorded at three to four day intervals for 40 days. Viability of pads (i.e. presence of roots and/or firm green tissue) was recorded.

At the end of the experiment, pads from the still water were air-dried at 22°C for two months to determine their drought tolerance. Viability and vegetative growth (i.e. new pads) were recorded.

(b) Geochory and epizoochory. In May 1981, 30 marked one-year-old pads were placed on a $1m^2$ rock surface at the maximum height above water at which cactus colonies occurred. In October 1981 and June 1982, the terrestrial dispersal of the pads was recorded as distance travelled, substrate where deposited, and viability.

2. Establishment

The effects of microhabitat on survival, root production, and growth were measured from May 1981 to June 1982, using 300 marked one-year-old pads. Groups of five pads, protected by wire mesh cages, were subjected to combinations of the following environmental factors in a randomized block design (Table 3.1):

(a) aspect (either north- or south-facing),

(b) canopy (either present -- balsam fir/white spruce forest, or absent -- open rock outcrop), and

(c) substrate (either bare soil, moss mat, or herb mat). Moss mats were continuous swards to six cm deep, comprised

Table 3.1: Experimental design for establishment experiments.

Variable	Treatment											
Aspect:	South-facing						North-facing					
Canopy:	Present			Absent			Present			Absent		
Substrate:	Soil	Moss	Herb	Soil	Moss	Herb	Soil	Moss	Herb	Soil	Moss	Herb
# cages	5	5	5	5	5**	5	5	5	5	5	5	5
# pads	25	25	25	25	25*	25*	25*	25*	25	25*	25*	25*

* indicates loss of single pad; **loss of two cages.

mostly of *Tortula ruralis* and *Hedwigia ciliata*. Herb mats consisted of pure or mixed stands of *Carex* species, low grasses, and scattered individual forbs such as *Achillea millefolium*.

There were five replicates of each treatment.

In October 1981 and June 1982, the number of pads in each of the following categories was noted:

(a) alive, rooted, with new pads,
(b) alive and rooted, without new pads,
(c) alive, without roots and new pads,
(d) dead, or
(e) lost.

Soil samples from beneath each cage were analyzed at the Manitoba Provincial Testing Laboratory for pH, conductivity, organic, moisture, and macronutrient contents using the standard procedures of McKeague (1978). Bulk density was calculated (Jeffrey 1970).

The relationship between establishment and environment was tested using a three-way test of independence (G-test, Sokal and Rohlf 1969). The G-test is analogous to analysis of variance but used for frequency data. It was used to test association between the environmental factors (aspect, canopy, and substrate) and each of the following:

(a) the number of surviving pads (a, b, and c above),
(b) the number of rooted pads (a and b above), and
(c) the number of pads which had produced new pads (a above).

Raw data from 1981 and 1982 were tested separately.

Three-way analysis of variance (Sokal and Rohlf 1969) was used to test for variation in mean soil characteristics with aspect, canopy, and substrate. When variation was significant ($P < 0.05$), the Student's t-test (Sokal and Rohlf 1969) was used to locate the specific differences.

3. Maintenance

Population structure and dynamics of an established colony were obtained by comparing pad censuses of the Bird River colony in October 1979, October 1981, and June 1982. The latter included 1982's new pad production. The number of pads in each of four states was recorded:

(a) established -- any pad attached to at least one pad, either one having roots. These were categorized as either less than, or greater than one year old,

(b) rooted -- single pad with roots,

(c) free -- single pad without roots, or

(d) dead.

Results

1. Dispersal

Pads were capable of dispersal by all the methods tested.

Hydrochory. All pads in still water were intact, buoyant, and had produced roots after 40 days. Ninety-five percent produced new pads within ten days. After two months air-drying, 60% of the original pads and 100% of the new pads were viable. No pads were produced during drying.

Pads in agitated water remained buoyant except when ruptured by violent agitation (20%) or fungus (15%). Pad rupture occurred from day 14 onward. After 40 days, 20% had produced roots, but none had produced new pads. Broken root stubs were observed at the lower nodes, and the spines on all pads were broken and blunted.

Pads floating in the river at the study site were observed to lodge in crevices or moss on the shoreline. These pads had intact spines but neither roots nor new pads.

Geochory and epizoochory. In October 1981, 21 of the 30 pads had not been recovered, and presumably had been dispersed from the outcrop. Nine pads were located a mean of 5.1 m (range of 1.8 to 15.0 m) downhill from the centre of placement. Two of the nine were anchored in organic litter in a patch of grass, and seven in mats of *Tortula ruralis*. All were green and turgid. Four had produced new pads.

By June 1982, the pads in grass had died, however those in *Tortula* mats were still green, turgid, and another two had produced new pads. Survival of free pads on the outcrop is estimated at:

$$\frac{7}{30-2} = 25\%$$

Disturbed pads rolled down rock slopes until their spines anchored in moss mats or soil. Small clumps of cacti were located below large older ones on the slope. Pads often adhered to humans (e.g. shoes or pant cuffs). Individual pads were found on trails in the forest, but showed no sign of root or new pad production and none survived more than one growing season under the forest canopy.

2. Establishment

Successful establishment was defined as viability, root and new pad production. The following differences were significant ($P < 0.05$).

Pad survival ranged from 63% to 100% per treatment, with a total of 93.6% after 11 months (Table 3.2). Analysis of October 1981 and June 1982 data showed that survival was affected by an interaction between aspect and substrate (Appendix 3.1). On both aspects, survival was highest on moss mats. On the south-facing shore, it was equally high on bare soil, whereas on the north-facing shore, it was also high on herb mats.

In October 1981, 83% of the pads had produced roots (Table 3.3), but root production was higher on moss mats and bare soil than on herb mats (Appendix 3.1). By June 1982, root production was independent of all three factors.

By October 1981, 68.2% of the living pads had produced new pads (Table 3.4), and this was related to aspect, canopy, and substrate (Appendix 3.1). More were formed on the south-facing shore than the north-facing, and on outcrops as opposed to forest. On the south-facing outcrop, new pad production on moss mats and bare soil was double that on herb mats. This difference did not occur under the forest canopy.

The production of pads in the second growing season was considered the best criterion for establishment because it represented new growth, and it was less likely to depend on the previous year's stored materials than pad production in the

Table 3.2: Percentages of pads recovered in a viable state grouped according to aspect, canopy, and substrate. Values are for June 1982; those enclosed in parentheses are for October 1981. N = 300

Aspect	Substrate	Canopy		
		Absent	Present	Both Canopies
North-facing	Moss	(92.0) 92.0	(100.0) 100.0	(95.5) 95.7
	Herb	(100.0) 100.0	(96.0) 95.8	(98.0) 90.9
	Soil	(95.8) 100.0	(75.0) 80.0	(85.4) 98.0
	All substrates	(95.9) 97.3	(89.9) 92.4	(91.9) 95.0
South-facing	Moss	(100.0) 66.7	(96.0) 88.0	(97.6) 90.0
	Herb	(63.2) 79.2	(96.0) 96.0	(81.8) 87.8
	Soil	(92.0) 96.3	(100.0) 100.0	(96.0) 98.1
	All substrates	(85.2) 89.4	(97.3) 94.7	(91.9) 92.2
Combined Aspects	Moss	(95.2) 92.5	(97.8) 93.6	(96.6) 93.1
	Herb	(84.1) 89.8	(96.0) 95.9	(90.4) 92.9
	Soil	(93.9) 98.0	(87.8) 91.1	(90.8) 94.8
Combined Aspects and Substrates		(91.1) 93.6	(93.8) 93.6	(92.5) 93.6

Table 3.3: Percentages of living pads that had produced roots by June 1982. Values in parentheses are for October 1981.

Aspect	Substrate	Canopy		
		Absent	Present	Both Canopies
North-facing	Moss	(82.6) 87.0	(90.0) 81.8	(86.0) 84.4
	Herb	(91.3) 68.0	(94.4) 91.3	(92.7) 79.2
	Soil	(72.0) 91.7	(87.5) 75.0	(79.6) 85.0
	All substrates	(81.7) 81.9	(90.3) 83.6	(85.7) 82.7
South-facing	Moss	(100.0) 100.0	(87.5) 81.8	(92.7) 88.9
	Herb	(100.0) 68.4	(84.0) 83.3	(91.7) 76.7
	Soil	(58.3) 92.3	(75.0) 88.0	(69.4) 90.2
	All substrates	(90.4) 86.4	(82.2) 84.5	(85.6) 85.4
Combined Aspects	Moss	(90.0) 91.9	(88.6) 81.8	(89.3) 86.4
	Herb	(67.6) 92.0	(81.3) 82.9	(75.3) 87.9
	Soil	(95.7) 68.2	(88.4) 87.2	(92.1) 78.0
Combined Aspects and Substrates		(85.4) 84.0	(85.9) 84.1	(85.7) 84.0

Table 3.4: Percentages of living pads that produced new pads in the June 1982 growing season. Values in parentheses are for October 1981.

Aspect	Substrate	Canopy					
		Absent		Present		Both Canopies	
North-facing	Moss	(73.9)	17.4	(50.0)	18.2	(62.8)	17.8
	Herb	(82.6)	24.0	(55.6)	43.5	(70.7)	33.3
	Soil	(44.0)	29.2	(58.3)	25.0	(51.0)	27.5
	All substrates	(66.2)	23.6	(54.8)	29.5	(60.9)	26.3
South-facing	Moss	(94.1)	100.0	(70.8)	18.2	(80.5)	50.0
	Herb	(95.7)	52.6	(68.0)	50.0	(81.3)	51.2
	Soil	(58.3)	84.0	(61.7)	44.0	(63.9)	64.0
	All substrates	(86.5)	77.6	(68.5)	38.0	(76.0)	55.8
Combined Aspects	Moss	(82.5)	48.6	(61.4)	18.2	(71.4)	65.9
	Herb	(89.1)	36.4	(62.8)	46.8	(76.4)	70.3
	Soil	(48.6)	57.1	(62.5)	36.6	(56.5)	82.0
Combined Aspects and Substrates		(74.8)	47.7	(62.2)	34.1	(68.2)	40.8

first season. In June 1982, pad production was related to aspect, canopy, and substrate (Appendix 3.1), but fewer new pads were produced (Table 3.4). Pad production was higher on the south-facing shore than on the north-facing shore. On the south-facing shore, more new pads were produced on outcrops than under a canopy, however this difference did not occur on the north- facing shore. The advantage of moss mats or bare soil as a substrate for new pad production did not recur in 1982, and surprisingly, herb mats were the best substrates under the canopy.

Sample size was altered in October 1981, when 21 pads had been lost (Table 3.1). Two cages on the south-facing shore were accessible and had presumably been disturbed by fishermen. By June 1982, one lost cage was found but five other pads were lost. In October 1981, 7.5% of the remaining pads were dead. Four had produced new pads before dying, hence only 6.4% of the recovered pads were recorded as dead in June 1982.

Soil properties were variable (Appendix 3.2). Available phosphorous (mean value 8.74 $\pm$ 10.10 kg/ha) and potassium (94.87 $\pm$ 37.55 kg/ha) did not differ with aspect, canopy, or substrate ($P > 0.05$, Appendix 3.3). Significant variation ($P < 0.05$) in the remaining soil properties (Appendix 3.3) is summarized below:

(a) pH. All soils were acidic (mean value 5.3 $\pm$ 0.5). Soil pH was lower in north-facing than south-facing habitats, especially in the forest.

(b) Conductivity. Conductivity ranged from 0.10 to 0.28 mmhos/cm (mean value 0.17 ± 0.06 mmhos/cm). It was lower in north-facing soils than south-facing.

(c) Organic content. All soils were highly organic (up to 69.6% by weight). Outcrop soils had lower organic contents than forest soils.

(d) Moisture content. Soil moisture was variable (mean value 50.11 ± 14.36% by weight). Moisture content was lower in soils on outcrops than in the forest. It was also lower in bare soils than in soils under moss or herb mats.

(e) Bulk density. All of the soils had low bulk densities (mean value 0.39 ± 0.19 g/ml). Density of forest soils was lower than that of outcrop soils.

3. Maintenance

The number of living pads in the Bird River colony increased at a mean rate of 31.3% for each of four years (Table 3.5). The net increase of 31.8% between 1981 and 1982 included the loss of 14% of the new pads, which had been removed in August 1981 for experiments.

At least 90% of the colony was composed of established pads, while the remaining 10% were free or rooted pads. Approximately 50% of all pads were new. The proportion of pads dispersed from the outcrop each year was roughly estimated using the results from the dispersal experiments:

Table 3.5: Pads of various categories in a colony of *Opuntia fragilis* at Bird River.

Date		Pad State						Total living	% increase/yr.
		Established			Free	Rooted	Dead		
		< 1 year	> 1 year	Total					
May 1982	#	755	1065	1820	44	26	117	1890	31.8%
	(%)	(39.9)	(56.3)	(96.3)	(2.3)	(1.4)		(100)	
October 1981	#	757	423	1180	77	32	49	1289**	22.7%
	(%)	(58.7)	(32.8)	(91.5)	(6.0)	(2.5)		(100)	
October 1979	#	278	375	653	32	20	--	705	39.4%
	(%)	(39.4)	(53.2)	(92.6)	(4.5)	(2.8)	--	(100)	
Estimate 1978 *	#	--	--	--	--	--	--	427	
Mean % (1979 - 1982)					(4.3)	(2.2)			31.3%

* estimate of minimum total from 1978 = (total 1979) - (# pads ≤ 1 year old)
= 705 - 278 = 427

** 186 one-year-old pads were removed during experiments late in 1981, reducing the total to 1103.

(a) $\dfrac{\text{\% pads rooted}}{\text{\% pads dispersed}} = \dfrac{7}{21} = 0.33$ (from page 77)

(b) $\dfrac{\text{Mean \% pads rooted}}{\text{Mean \% pads dispersed}} = \dfrac{\dfrac{1.4 + 2.5 + 2.8}{3}}{\text{mean \% pad dispersed}} = 0.33$ (from Table 3.5)

(c) Mean % pads dispersed $= \dfrac{\dfrac{1.4 + 2.5 + 2.8}{3}}{0.33} = \dfrac{2.23}{0.33} = 6.77\%$ per year

Discussion

Harper (1939) stated that "it is one of the great mysteries of nature how the species known only on rock outcrops ... could have found their way to isolated localities many miles from other similar habitats." Information on the migrational capacity and barriers (*sensu* Cain 1944) of individual species may shed light on the historical migration routes, time of arrival, status (i.e. relic, invader), and restrictions of outcrop vegetation.

Dispersal

Pads of *Opuntia fragilis* are adapted to three dispersal mechanisms:

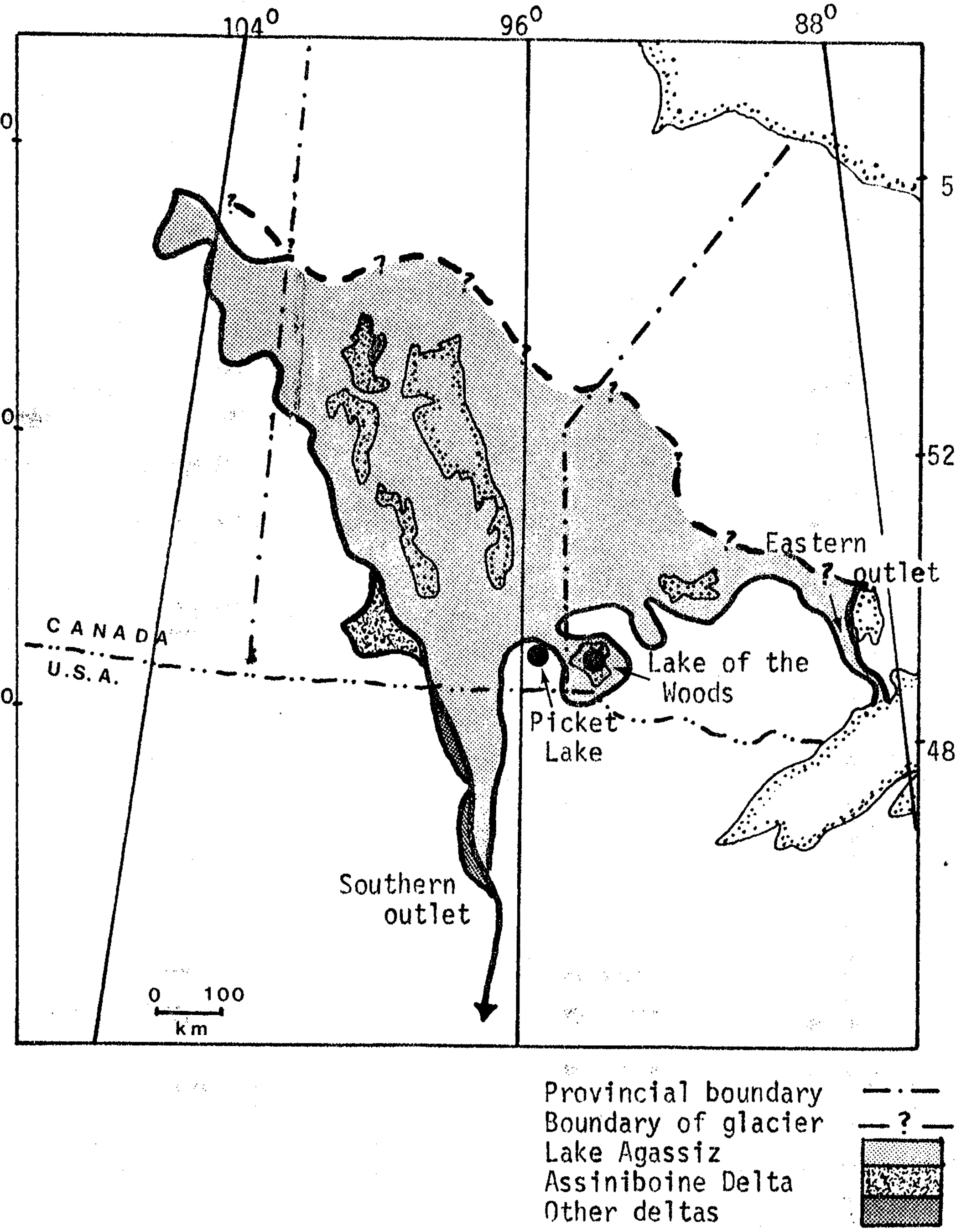
1. Geochory. The terminal pads are easily detached from the chain. They roll downhill on their spreading spines until the barbs anchor in soil or moss. This mechanism allows spread within an outcrop with little risk.

2. Hydrochory. Unanchored pads may roll into the river, where they float for long periods. The spines protect pads unless they are broken by prolonged turbulence. The barbs anchor on banks where the pads can survive prolonged drought. This mechanism allows long-distance dispersal, but carries more risk and restricts colonization to downstream water-edge sites.
3. Epizoochory. Spines may anchor in animals, and also protect the pad from damage by the animal. This mechanism may function over long distances, but restricts colonization to animal trails. There is considerable risk that most pads will be deposited in unsuitable habitats.

These mechanisms are functions of propagule morphology and presumably apply to both pads and dry spiny fruits, and have been operative in sexually and/or vegetatively reproducing post-glacial populations. Original colonization and spread in Manitoba involving these mechanisms have been hypothesized for three periods:

1. 9,000-7,500 years BP. Propagules may have been introduced into Lake Agassiz II by herd mammals from the west, and deposited along the shores (Fig. 3.1). This hypothesis is supported by the presence of _Opuntia fragilis_ and other grassland species on the Assiniboine Delta (southwestern Manitoba), southern outlet (Red and Missouri River Valleys), and eastern spillways (Lake of the Woods and Kaladar, Ontario). From 8,000 to 7,000 BP, open pine forest occurred at Picket Lake (Buchner 1981) which indicates dry land and a climate warm enough for _Opuntia_ colonization.

Figure 3.1: Approximate extent of Lake Agassiz (9000 - 7500 years BP) with sites mentioned in text. Modified from Elson (1967).

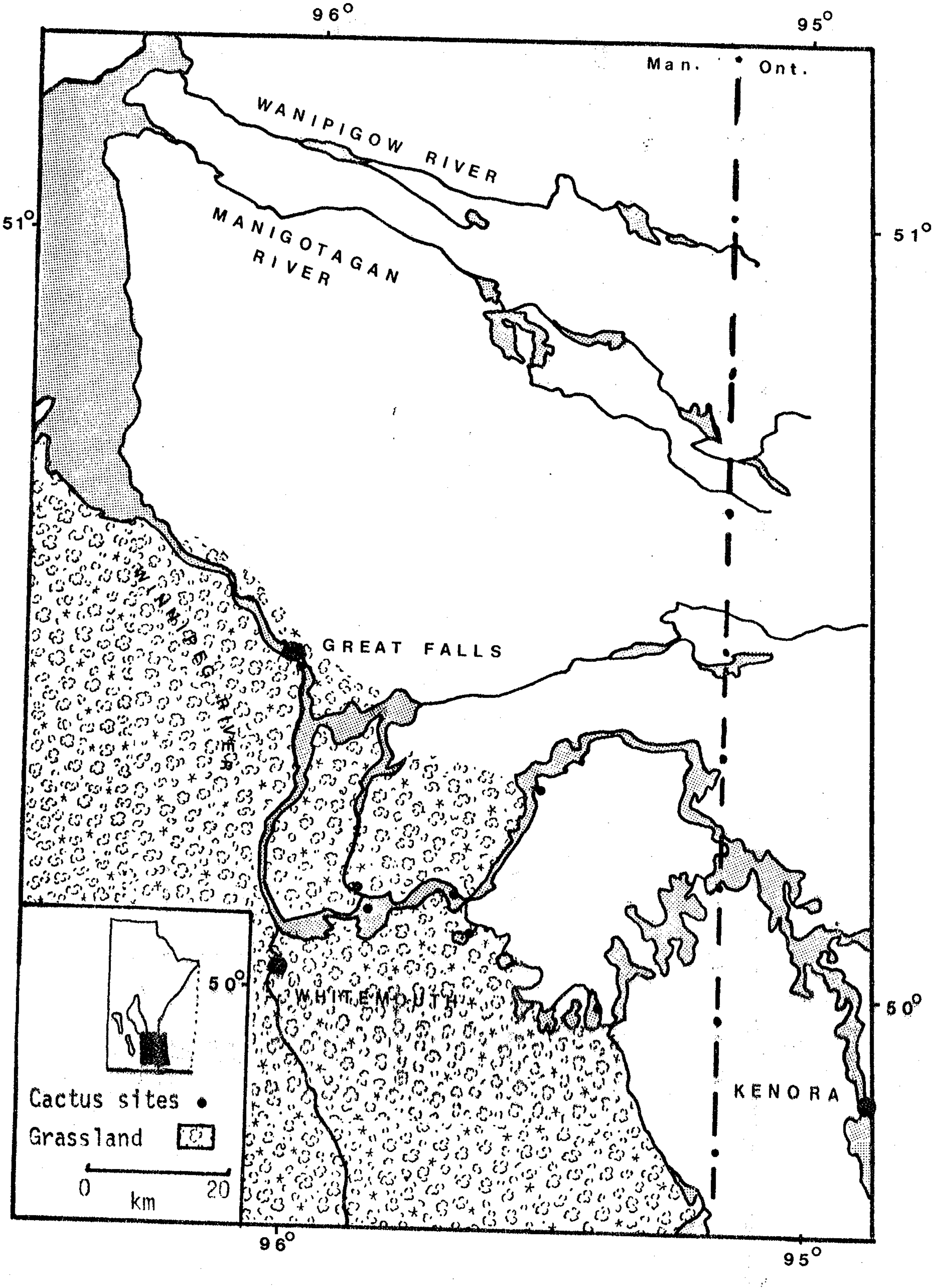

104°
96°
88°
56°
56°
52°
52°
48°
48°
CANADA
U.S.A.
Eastern outlet
Lake of the Woods
Picket Lake
Southern outlet
0 100
km
Provincial boundary
Boundary of glacier
?
?
Lake Agassiz
Assiniboine Delta
Other deltas

This may account for the origin of scattered colonies which spread during later periods, but predicts (a) land-locked colonies, and (b) colonies near e.g. Riding Mountain, exposed during the same period.

2. 7,500-4,000 BP. Opuntia fragilis may have entered Manitoba during the warm dry Altithermal Period (sensu Antevs 1948). Grassland may have extended to the Winnipeg River (Buchner 1981), and bison migrated to Great Falls (Steinbring 1970), Whitemouth (Buchner and Pujo 1977), and Kenora (McAndrews 1980; Fig. 3.2). Cacti may have reached the grassland/oak grove mosaic northeast of the Winnipeg River (Buchner 1981) by epizoochory. Propagules may have been further dispersed by Indians who penetrated the forest to the Wanipigow/Manigotagan River at the end of the Altithermal (Buchner 1981). This hypothesis is supported by (a) the concentration of colonies on the Winnipeg River system (Chapter II), and (b) the occurrence of similarily restricted grassland species on the outcrops.
3. 4,000 BP - Present. Propagules may have been dispersed to outcrops in the boreal forest by voyageurs or Indians, either accidentally (e.g. on bales of fur) or purposely (e.g. for food or technology -- see Szczawinski and Turner 1980). This would account for colonies further upstream. This hypothesis is supported by (a) restriction to waterways, especially on portages of canoe routes, and (b) presence of other useful species (e.g. Allium stellatum, Densmore 1928).

Data are insufficient to date the arrival of Opuntia fragilis. In view of its absence from land-locked sites, it seems likely that hydrochory and/or human dispersal along canoe routes has maintained

Figure 3.2: Approximate location of vegetation zones in southeastern Manitoba during the Altithermal Period. Modified from Buchner (1981).


96°
95°
Man.
Ont.
WANIPIGOW RIVER
MANIGOTAGAN RIVER
51°
51°
WINNIPEG RIVER
GREAT FALLS
50°
50°
WHITEMOUTH
KENORA
Cactus sites ●
Grassland
0
km
20
96°
95°

its present distribution.

Establishment

Knowledge of present dispersal mechanisms suggests that pads will arrive on shores of rivers or lakes, on portages, and along animal trails. Placement of pads in representative habitats, while monitoring survival and growth, determines the ultimate success of the dispersal phase.

The best criterion of establishment, pad production during the second growing season, was highest on south-facing outcrops. Since success was unaffected by substrate, the advantage of this habitat over forest or north-facing slopes presumably involves _Opuntia_'s requirement for higher temperature and light intensity (Chapter II, Rejmanek 1971). Pads grown in the forest or artificial light (e.g. environmental chamber) were weak and etiolated. New pads retained their leaves and their spines were short and weak.

Higher temperatures on outcrops extend the growing season (Chapter II), which can be utilized by the evergreen cactus stem. Because the snow melts earlier in this habitat, the seasonal growth of _Opuntia fragilis_ coincides with the period of highest moisture availability. During the rest of the season, the pads' succulence and thick cuticle (Chapter I) tolerate the drought caused by shallow soil, high degree of runoff, and exposure to wind and sun. _Opuntia fragilis_ may benefit from the minor disturbance to which south-facing outcrops are susceptible. Erosion of moss mats (c.f. Oosting and Anderson 1937) and breakage by animals may aid in dispersal. Extreme disturbance such as trampling or fire may eliminate the cactus.

Maintenance in an Established Population

Established colonies serve as sources for colonization of other outcrops (e.g. downstream) as well as expansion within an outcrop; hence maintenance of these colonies is critical.

The colony at Bird River has been known for nearly 20 years, and contains individual chains of pads aged at 11 years. In 1982, the colony consisted of nearly 2,000 pads in 32 clumps. The net number of pads increased by approximately 30% per year. Half the colony was composed of new pads which have the potential to detach and disperse. There is no estimate of the frequency of detachment, but 2.2-6.5% of the pads formed new clumps on the same outcrop, while an estimated 6.8% were dispersed from the outcrop.

The colony may be eliminated by the development of a dense canopy but the persistence of outcrops in this region since ca. 9,000 BP suggests that the formation of a canopy is a very slow process.

Conclusions

Long-distance dispersal by epizoochory and hydrochory has the potential to increase the distribution of *Opuntia fragilis*, but pads survive only on south-facing outcrops. The cactus is apparently absent from land-locked outcrops. It does not appear to be in danger of elimination from the outcrops on which it is established. These observations suggest that *O. fragilis* is both habitat and dispersal limited.

Appendix 3.1: G-test tables of three pad states (S): survival, rooting, and new pad production, in (1) 1981, and (2) 1982, according to aspect (A), canopy (C), and substrate (Sub). * indicates significance at P = 0.05, n.s. = not significant.

	Hypothesis	df	G	
(1) 1981 Pad Survival	A x Sub independence	2	0.36	n.s.
	A x S independence	1	0.12	n.s.
	Sub x S independence	2	3.46	n.s.
	A x Sub x S interaction	2	11.46	*
	A x Sub x S independence	7	15.36	*
	A x C x S independence	4	6.04	n.s.
	C x Sub x S independence	7	9.18	n.s.
Pad Rooting	A x Sub independence	2	2.34	n.s.
	A x S independence	1	0.00	n.s.
	Sub x S independence	2	10.84	*
	A x Sub x S interaction	2	2.18	n.s.
	A x Sub x S independence	7	15.34	*
	A x C x S independence	4	7.36	n.s.
	C x Sub independence	2	1.16	n.s.
	C x S independence	1	0.00	n.s.
	Sub x S independence	2	10.84	*
	C x Sub x S interaction	2	3.80	n.s.
	C x Sub x S independence	7	15.80	*
New Pad Production	A x C independence	1	3.58	n.s.
	C x S independence	1	4.72	*
	A x S independence	1	6.82	*
	A x C x S interaction	1	2.80	n.s.
	A x C x S independence	4	17.92	*
	A x Sub independence	2	2.34	n.s.
	A x S independence	1	6.82	*
	Sub x S independence	2	8.44	*
	A x Sub x S interaction	2	-0.80	n.s.
	A x Sub x S independence	7	16.80	*
	C x Sub independence	2	1.16	n.s.
	C x S independence	1	4.72	*
	Sub x S independence	2	8.44	*
	C x Sub x S interaction	2	10.46	*
	C x Sub x S independence	7	24.78	*

Continued ...

Appendix 3.1 (continued):

(2) 1982	Hypothesis	df	G	
Pad Survival	A x C x S	4	5.10	n.s.
	C x Sub x S	7	5.22	n.s.
	A x Sub x S	7	9.54	n.s.
Pad Rooting	A x C x S independence	4	6.68	n.s.
	C x Sub x S independence	7	13.74	n.s.
	A x Sub x S independence	7	7.24	n.s.
New Pad Production	A x C x S independence	4	6.42	n.s.
	A x Sub independence	2	2.34	n.s.
	Sub x S independence	2	4.46	n.s.
	A x S independence	1	24.00	*
	A x Sub x S interaction	2	0.80	n.s.
	A x Sub x S independence	7	31.60	*
	C x Sub independence	2	1.42	n.s.
	C x S independence	1	5.04	*
	Sub x S independence	2	4.46	n.s.
	C x Sub x S interaction	2	8.46	*
	C x Sub x S independence	7	19.38	*

Appendix 3.2: Characteristics of soils from two aspects (north- or south-facing), two canopies (bare rock outcrop or mixed coniferous forest), and three substrates (moss, mat, herb mat, or bare soil). Values are mean ± 1 s, n = 300.

Soil Characteristics	Aspect	Substrate	Canopy		Both Canopies
			Absent	Present	
a) pH	North-facing	Moss	5.0 ± 0.4	4.7 ± 0.1	4.9 ± 0.3
		Soil	4.9 ± 0.2	5.0 ± 0.3	5.0 ± 0.2
		Herb	5.1 ± 0.4	4.7 ± 0.2	4.9 ± 0.3
		All substrates	4.9 ± 0.3	4.9 ± 0.3	4.9 ± 0.3
	South-facing	Moss	5.3 ± 0.1	5.3 ± 0.4	5.3 ± 0.3
		Soil	5.1 ± 0.5	6.1 ± 0.4	5.6 ± 0.6
		Herb	5.7 ± 0.2	5.9 ± 0.5	5.8 ± 0.4
		All substrates	5.4 ± 0.5	5.8 ± 0.6	5.6 ± 0.5
	Both Aspects	Moss	5.1 ± 0.3	5.0 ± 0.4	5.1 ± 0.4
		Soil	5.0 ± 0.4	5.5 ± 0.6	5.5 ± 0.5
		Herb	5.5 ± 0.4	5.4 ± 0.7	5.4 ± 0.6
	TOTAL		5.2 ± 0.4	5.3 ± 0.6	5.3 ± 0.5
b) Conductivity (mmhos/cm)	North-facing	Moss	0.14 ± 0.05	0.10 ± 0.00	0.13 ± 0.05
		Soil	0.10 ± 0.00	0.16 ± 0.09	0.13 ± 0.07
		Herb	0.17 ± 0.06	0.13 ± 0.05	0.14 ± 0.05
		All substrates	0.13 ± 0.00	0.13 ± 0.00	0.13 ± 0.06
	South-facing	Moss	0.15 ± 0.07	0.20 ± 0.00	0.19 ± 0.04
		Soil	0.22 ± 0.08	0.28 ± 0.10	0.24 ± 0.09
		Herb	0.18 ± 0.05	0.24 ± 0.05	0.21 ± 0.06
		All substrates	0.21 ± 0.00	0.22 ± 0.10	0.22 ± 0.07
	Both Aspects	Moss	0.15 ± 0.05	0.16 ± 0.05	0.15 ± 0.05
		Soil	0.16 ± 0.08	0.21 ± 0.11	0.18 ± 0.10
		Herb	0.17 ± 0.05	0.19 ± 0.08	0.18 ± 0.07
	TOTAL		0.16 ± 0.06	0.19 ± 0.08	0.17 ± 0.06

Continued

Appendix 3.2, continued:

Soil Characteristics	Aspect	Substrate	Canopy		
			Absent	Present	Both Canopies
c) Organic Content (%)	North-facing	Moss	41.50 ± 20.26	69.60 ± 4.95	54.15 ± 19.56
		Soil	34.14 ± 14.00	33.74 ± 25.45	33.94 ± 19.36
		Herb	46.13 ± 14.74	67.80 ± 18.37	60.38 ± 17.00
		All substrates	40.59 ± 16.57	57.05 ± 18.35	49.49 ± 21.37
	South-facing	Moss	35.70 ± 28.43	53.65 ± 13.39	45.77 ± 17.67
		Soil	39.86 ± 18.07	46.52 ± 8.16	46.35 ± 17.42
		Herb	31.95 ± 9.97	58.96 ± 16.44	46.95 ± 19.37
		All substrates	36.50 ± 20.28	53.04 ± 13.12	43.36 ± 17.47
	Both Aspects	Moss	38.97 ± 19.24	60.27 ± 11.37	50.18 ± 18.67
		Soil	37.00 ± 15.53	43.30 ± 22.38	40.15 ± 19.02
		Herb	42.54 ± 17.77	64.35 ± 16.53	54.02 ± 18.94
	TOTAL		39.41 ± 16.13	55.97 ± 19.14	46.11 ± 18.43
d) Moisture Content (%)	North-facing	Moss	46.46 ± 12.39	65.17 ± 4.27	56.90 ± 14.07
		Soil	41.02 ± 14.22	42.18 ± 16.19	41.60 ± 14.38
		Herb	61.93 ± 9.52	64.43 ± 7.72	62.79 ± 6.96
		All substrates	50.13 ± 14.44	57.39 ± 15.02	53.76 ± 14.94
	South-facing	Moss	41.90 ± 12.87	58.80 ± 14.54	56.18 ± 14.13
		Soil	40.64 ± 5.99	52.05 ± 5.87	48.28 ± 11.21
		Herb	33.57 ± 10.38	60.66 ± 4.02	48.62 ± 15.88
		All substrates	40.57 ± 11.49	58.87 ± 29.08	50.73 ± 13.71
	Both Aspects	Moss	47.70 ± 12.93	63.68 ± 9.86	56.58 ± 13.68
		Soil	40.83 ± 10.29	49.05 ± 14.62	44.94 ± 13.01
		Herb	49.88 ± 17.44	61.66 ± 5.92	56.08 ± 13.75
	TOTAL		45.88 ± 13.84	58.13 ± 12.28	50.11 ± 14.36

Continued

Appendix 3.2, continued:

Soil Characteristics	Aspect	Substrate	Canopy		
			Absent	Present	Both Canopies
e) Available Phosphorous (kg/ha)	North-facing	Moss	4.59 ± 1.94	4.81 ± 1.18	5.09 ± 1.87
		Soil	3.65 ± 1.12	29.01 ± 24.86	16.33 ± 21.31
		Herb	13.21 ± 5.21	5.71 ± 4.03	7.60 ± 5.23
		All substrates	7.15 ± 4.01	13.18 ± 17.83	9.67 ± 13.21
	South-facing	Moss	7.35 ± 0.63	8.28 ± 3.45	7.73 ± 3.64
		Soil	9.70 ± 3.07	5.96 ± 1.47	7.84 ± 2.96
		Herb	3.72 ± 1.18	5.98 ± 1.77	4.97 ± 1.76
		All substrates	6.92 ± 2.37	6.74 ± 2.93	6.88 ± 3.09
	Both Aspects	Moss	6.03 ± 3.55	6.29 ± 3.78	6.34 ± 3.08
		Soil	6.68 ± 3.87	17.50 ± 20.56	12.09 ± 15.43
		Herb	7.21 ± 5.29	5.59 ± 2.75	6.36 ± 4.11
	TOTAL		6.64 ± 4.15	9.90 ± 12.89	8.74 ± 10.10
) Available Potassium (kg/ha)	North-facing	Moss	82.26 ± 26.38	73.18 ± 19.82	89.75 ± 30.95
		Soil	63.58 ± 11.82	113.76 ± 31.75	88.67 ± 34.78
		Herb	133.64 ± 30.12	48.50 ± 5.40	86.26 ± 41.68
		All substrates	93.16 ± 29.52	78.48 ± 26.74	88.23 ± 34.84
	South-facing	Moss	81.29 ± 13.99	97.00 ± 10.26	94.08 ± 20.40
		Soil	99.76 ± 54.46	145.72 ± 43.21	115.45 ± 52.77
		Herb	106.69 ± 30.05	95.41 ± 44.28	110.42 ± 36.80
		All substrates	95.91 ± 46.30	112.71 ± 44.35	103.75 ± 39.22
	Both Aspects	Moss	88.99 ± 24.46	91.18 ± 29.98	91.80 ± 25.87
		Soil	81.67 ± 42.92	122.46 ± 40.33	102.06 ± 45.62
		Herb	114.88 ± 27.92	73.25 ± 37.97	92.97 ± 39.03
	TOTAL		94.70 ± 35.52	96.68 ± 39.87	94.87 ± 37.55

Continued

Appendix 3.2, continued:

Soil Characteristics	Aspect	Substrate	Canopy Absent	Canopy Present	Both Canopies
g) Bulk Density (gm/ml)	North-facing	Moss	0.43 ± 0.20	0.23 ± 0.02	0.34 ± 0.17
		Soil	0.47 ± 0.14	0.58 ± 0.37	0.52 ± 0.27
		Herb	0.36 ± 0.11	0.25 ± 0.09	0.29 ± 0.09
		All substrates	0.42 ± 0.19	0.35 ± 0.27	0.38 ± 0.21
	South-facing	Moss	0.48 ± 0.27	0.32 ± 0.08	0.38 ± 0.15
		Soil	0.44 ± 0.21	0.35 ± 0.06	0.38 ± 0.16
		Herb	0.47 ± 0.09	0.29 ± 0.08	0.37 ± 0.12
		All substrates	0.46 ± 0.25	0.32 ± 0.09	0.38 ± 0.14
	Both Aspects	Moss	0.45 ± 0.19	0.28 ± 0.06	0.36 ± 0.16
		Soil	0.45 ± 0.17	0.45 ± 0.28	0.45 ± 0.23
		Herb	0.39 ± 0.11	0.26 ± 0.08	0.33 ± 0.12
	TOTAL		0.43 ± 0.15	0.33 ± 0.19	0.39 ± 0.19

Appendix 3.3: Analysis of variance tables for soil variables under different cages, according to aspect (A), canopy (C), and substrate (S). * indicates a significant difference at $P < 0.05$.

Soil Variable	Source of Variation	df	Sum of Squares	Mean Square	F-Statistic	
pH	A	1	5.06	5.06	43.26	*
	C	1	0.11	0.11	0.98	
	S	2	0.72	0.36	3.09	
	A x C	1	0.91	0.91	7.79	*
	A x S	2	0.34	0.17	1.47	
	C x S	2	1.15	0.58	4.92	*
	A x C x S	2	0.14	0.07	0.62	
	Error	37	4.33	0.12		
Conductivity	A	1	0.07	0.07	18.55	*
	C	1	0.01	0.01	1.86	
	S	2	0.01	0.01	1.74	
	A x C	1	0.01	0.01	3.11	
	A x S	2	0.01	0.00	1.31	
	C x S	2	0.01	0.00	0.91	
	A x C x S	2	0.01	0.00	1.04	
	Error	37	0.14	0.00		
% Organic Content	A	1	217.90	217.90	0.75	
	C	1	3220.84	3220.84	11.09	*
	S	2	1670.13	830.07	2.88	
	A x C	1	1.61	1.61	0.01	
	A x S	2	1180.20	590.10	2.03	
	C x S	2	1198.64	599.32	2.06	
	A x C x S	2	156.00	78.00	0.27	
	Error	37	10742.06	290.33		
% Moisture Content	A	1	355.67	355.67	3.06	
	C	1	1909.13	1909.13	16.42	*
	S	2	1212.21	606.11	5.21	*
	A x C	1	344.66	344.66	2.96	
	A x S	2	921.00	460.50	3.96	*
	C x S	2	288.43	144.22	1.24	
	A x C x S	2	305.48	152.74	1.31	
	Error	37	4302.39	116.28		

Continued

Appendix 3.3 (Continued):

Soil Variable	Source of Variation	df	Sum of Squares	Mean Square	F-Statistic	
Bulk Density	A	1	0.00	0.00	0.01	
	C	1	0.13	0.13	4.11	*
	S	2	0.13	0.06	2.09	
	A x C	1	0.02	0.02	0.57	
	A x S	2	0.11	0.05	1.77	
	C x S	2	0.09	0.05	1.46	
	A x C x S	2	0.02	0.01	0.40	
	Error	37	1.15	0.03		
Available Phosphorous	A	1	126.09	126.09	1.73	
	C	1	97.04	97.04	1.33	
	S	2	324.45	162.23	2.23	
	A x C	1	109.84	109.84	1.51	
	A x S	2	254.38	127.19	1.75	
	C x S	2	422.80	211.40	2.91	
	A x C x S	2	888.00	444.00	6.10	*
	Error	37	2692.52	72.77		
Available Potassium	A	1	3888.14	3888.14	3.64	
	C	1	12.76	12.76	0.01	
	S	2	3727.13	1863.56	1.75	
	A x C	1	2815.92	2815.92	2.64	
	A x S	2	1549.03	774.51	0.73	
	C x S	2	19695.15	9847.58	9.23	*
	A x C x S	2	3257.38	1628.69	1.53	
	Error	37	39476.55	1066.93		

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CHAPTER FOUR

Successional Sequence on Three Manitoban Outcrops and Position of *Opuntia fragilis*

ABSTRACT

The successional sequence on three outcrops containing *Opuntia fragilis* (Nutt.) Haw. was examined using physiography and species cover. Data were collected from June - August 1982 on five 10m line transects at each site. A successional sequence of species was predicted, based on their life-forms, strategies, and contribution to soil formation. Preliminary ordinations using reciprocal averaging/weighted averaging hybrids indicated that substrate depth was the major factor determining the species gradient, hence substrate depth was used to order samples in weighted averaging ordinations. The resulting species sequence was positively correlated with the predicted sequence ($P < 0.05$). The stages of the successional sequence were: (0) bare rock/pioneer lichens, (1) primary moss mat, (2) secondary moss and lichen mat, (3) tertiary mat, (4) stress-tolerant perennials, (5) perennial grasses and sedges, and (6) chamaephytes and phanerophytes. The species composition of stages 0 - 3 was consistent at all three sites. Variation in subsequent stages was presumably due to propagule availability.

The sequence was basically similar to that of Clements (1963) but local variations in pattern and rate of spread were related to factors which altered the rate of soil accumulation: slope, aspect, rock surface features, and disturbance.

Opuntia fragilis, a stress-tolerant perennial, was the first vascular plant to colonize secondary (occasionally tertiary) moss mats, where it was positively associated with such species as *Tortula ruralis* ($P < 0.05$). Cactus vigour was not correlated with soil or physiography ($P > 0.05$).

CHAPTER FOUR

Successional Sequence on Manitoban Outcrops and Position of *Opuntia fragilis*

Introduction

The outcrops on which *Opuntia fragilis* grows in southeastern Manitoba are mosaics of rock and vegetation. The vegetation ranges from thallophytes to phanerophytes, but not in the spatial continuum predicted by the classical model of succession (Clements 1963). *Opuntia fragilis* was usually found in moss mats, which constitute an early seral stage. These observations suggested the following questions:

1. What is the successional sequence on these outcrops? How does it compare to the classical model of lithosere succession?
2. What is the ecological position of *O. fragilis* in the sequence?

Methods and Materials

Selection of Study Sites

Three sites containing *Opuntia fragilis* were selected using the following criteria:

1. The colonies should represent the widest geographic range in the boreal region; also, they were located on three different river systems.
2. Outcrops should be undisturbed but sufficiently accessible for study.

The sites were (Fig. 2.1, Chapter II):

1. Post Island, Big Whiteshell Lake (50°06'N, 95°20'W) on the Whiteshell River, south Winnipeg River system,
2. Bird River (50°25'N, 95°41'W), 6km east of Lac du Bonnet, on the north Winnipeg River system, and
3. Bissett (51°02'N, 95°41'W) on the north shore of Rice Lake on the Wanipigow River.

Successional Sequence

At each site, five 10m transects extended down the rock slope, through at least one clump of Opuntia fragilis. Preliminary analysis using the maximum mean square technique (Kershaw 1973, Mueller-Dombois and Ellenberg 1974) showed vegetation patterns at 0.33m and 1.0m scales (Appendix 4.1). The transects were divided into 0.33m sample intervals, corresponding to the mean scale of thallophytes (c.f. Mueller- Dombois and Ellenberg 1974). Within each sample interval, cover for each species was measured at 2cm intervals by dropping a 1.5mm diameter pin through a frame, perpendicular to the rock. Substrate depth was measured using a calibrated rod; vertical height above water and slope were recorded by surveying.

The 150 blocks per site, labelled by number, were each termed a "sample" for the study. Two datasets were compiled: species percent cover per sample, and physiography per sample. The species cover and physiography values were transformed to a percentage of their maximum values to make different life-forms (sensu Raunkiaer 1937) and units of measure commensurate within a dataset (Gauch 1977).

The samples, species, and physiographic variables were arranged according to various measures of similarity using ordination

(Appendix 4.2). This technique was used to identify species communities, associations, or continua, and to relate the distribution of species to habitat physiography (Gauch 1977).

Two ordination techniques were performed on individual and combined site data, using the ORDIFLEX computer package (Gauch 1977):

1. Reciprocal Averaging/Weighted Averaging hybrid. In preliminary ordinations, the samples were arranged according to their similarities in species cover by reciprocal averaging, and their scores on two axes were used to weight the samples of the second dataset. Samples, species, and physiography were then plotted on common axes.
2. Weighted Averaging. Species were ordered on the first axis by weighting the samples with substrate depth. The choice of depth as a weight was based on literature (e.g. Winterringer and Vestal 1956), and on the results of the hybrid ordination above.

   Species were ordered on the second axis by their position in a predicted successional sequence (Table 4.1) based on life-form (Scoggan 1978), strategy (*sensu* Grime 1979), and contribution to soil formation.

   The species sequences for the individual sites were compared using Spearman's coefficient of rank correlation (Sokal and Rohlf 1969). The scores of "common" species (frequency > 10 out of 450 samples) from the combined sites were tested for correlation with the predicted sequence.

Position of *Opuntia fragilis*

Each clump of cactus encountered on the transects was further

Table 4.1: Predicted successional sequence according to life-form (Scoggan 1978)*, strategy (Grime 1979) and contribution to soil formation. Ranks were used to weight species for weighted averaging on first axis.

Predicted Rank in Sequence	Description	Species	
0.	"Pioneer lichen mat." No visible contributions to soil formation.	Bare rock low foliose lichens (e.g. Parmelia spp.)	crustose lichens low fruticose lichens (e.g. Cladonia pocillum
1.	"Primary moss mat". Primary colonizers of rock, initiators of soil formation.	Grimmia spp. Hedwigia ciliata	
2.	"Secondary mat". Mats which stabilize and/or generate organic debris.	Tortula ruralis Cladonia pyxidata	
3.	"Tertiary stage". Deeper mat on less than 1.5cm organic debris (often colonized by therophytes).	Polytrichum juniperum Cladina rangiferina C. mitis Cladonia amaurocraea	Thuidium abietinum Selaginella rupestris Ceratodon purpureus Peltigera rufescens
4.	"Stress-tolerant ruderals". Therophytes; do not alter environment, but require substrate > 2cm.	Panicum capillare Portulaca oleracea Cerastium nutans Geranium bicknellii	Polygonum convolvulus Potentilla norvegica Silene antirrhina
4.5	(Intermediate) Hemicryptophytes require shallow substrate, insignificant contribution to soil formation due to size and isolation.	Aquilegia canadensis Galium boreale Campanula rotundifolia	
5.	"Stress-tolerant perennials" crypto-, hemicrypto- or chamaephytes in deeper shallow substrate; either associated with mesic habitats (a), by root system (b), or collecting litter (c)	a) Agastache foeniculum b) Allium stellatum Agropyron trachycaulon Solidago missouriensis c) Woodsia ilvensis Opuntia fragilis Parthenocissus inserta	Achillea millefolium
6.	"Perennials grasses and sedges" with dense root or shoot mats: "real sod builders" (Hinds 1842)	Poa glauca Muhlenbergia spp. Andropogon gerardi	Polygonum douglasii
7.	Chamaephytes and phanerophytes with deep roots; collect and generate litter; provide canopy.	Juniperus spp. Prunus virginiana Amelanchier alnifolia Arctostaphylos uva-ursi Corylus americana	Crataegus chrysocarpa Corylus cornuta Populus tremuloides Apocynum androsaemifolium Symphoricarpos occidentalis

---

*Life-forms and contribution to soil formation of species ranked 0-3 are from Winterringer and Vestal (1956).

described by:

1. its size (total number of pads, number of pads < one year old),
2. pad characters (length, width, depth, fresh weight, and biomass; n = 20 one-year-old pads),
3. substrate depth at the centre of the clump, and
4. soil properties. A soil sample (10 x 10 x 6cm) was collected, frozen, and analyzed at the Manitoba Provincial Soil Testing Laboratory using the standard procedures (McKeague 1978) for pH, conductivity, organic, moisture, and macronutrient contents.

Comparisons were made between sites for mean pad and soil characters using analysis of variance and the Student's t-test (Sokal and Rohlf 1969). In addition, relationships between cactus vigour and substrate characters were tested using correlation coefficients. Samples were examined for species associations with cacti using chi-square (Sokal and Rohlf 1969).

Results*

Successional Sequence

Bare rock, bare soil, crustose lichens, *Hedwegia ciliata*, and *Tortula ruralis* were found at all three sites. Each site contained a small proportion of "localized" species which were absent from the other two sites: *Crataegus* spp., *Populus tremuloides*, *Prunus*

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*Species authorities are given in the species list (Appendix 4.3) and follow Scoggan (1978) for vascular plants, and Crum (1976) for mosses. Lichens were verified by P. Wong.

pensylvanica, P. pumila, and Andropogon gerardi at Bird River; Juniperus horizontalis and Portulaca oleracea at Bissett; and Bryum pseudotriquetrum, Polygonum douglasii, and Carex spp. at Big Whiteshell. All predicted seral stages (Table 4.1) were found at Bird River and Bissett; there were no chamaephytes or phanerophytes in the Big Whiteshell outcrop samples.

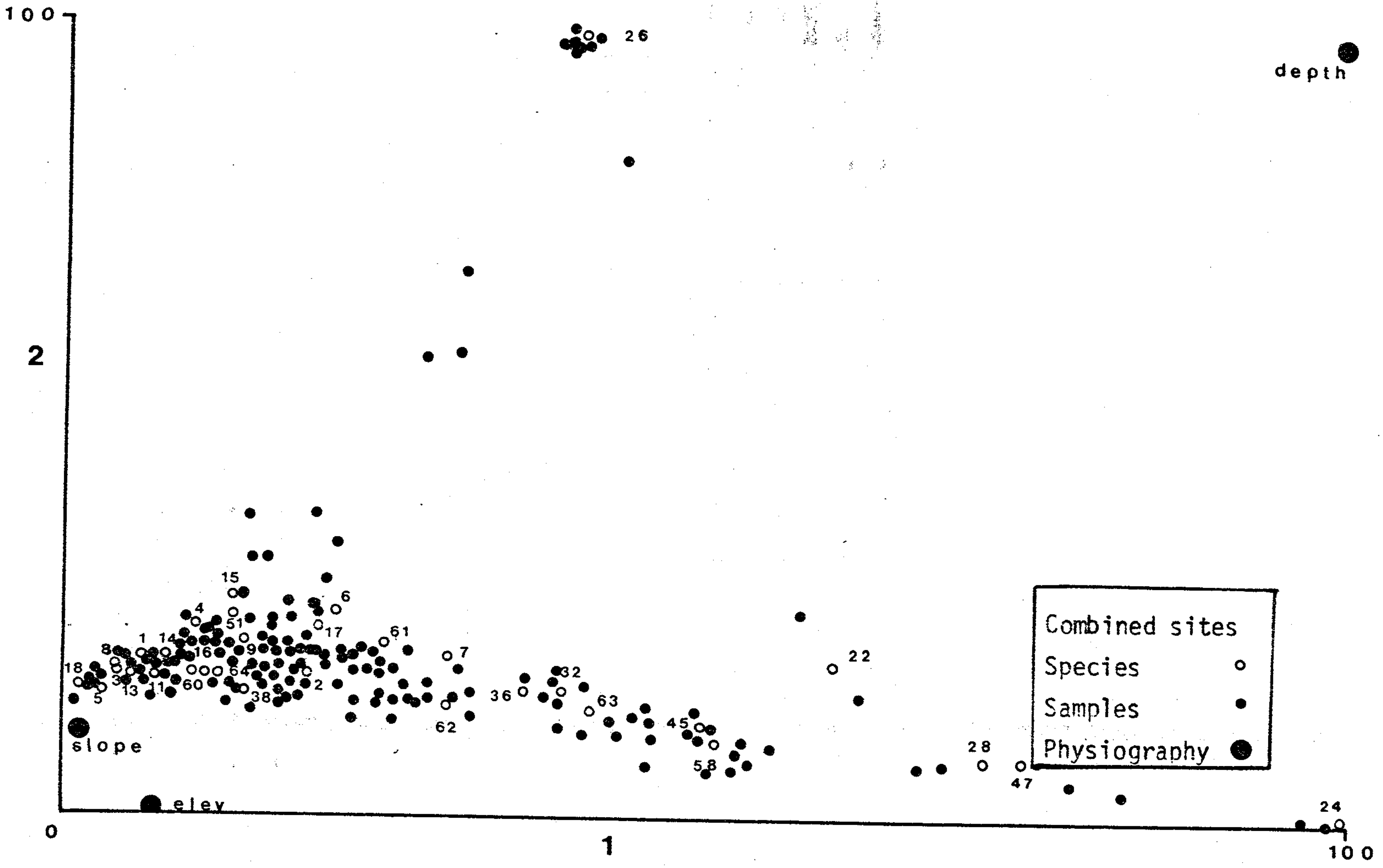
The following ordination results using combined site data apply equally well to individual site data which, for space considerations, have been placed in Appendix 4.4.

Reciprocal averaging alone explained less than half the dispersion of samples and species, i.e. the eigenvalues of the first two axes were less than 50% (Figure 4.1). Even inefficient ordinations are useful if they illustrate an ecological trend (van der Maarel 1980). In combination with weighted averaging, the ordination revealed three trends:

1. Low species richness was especially evident in disjunct samples. The isolated samples in Fig. 4.1 contained one or two taxa (e.g. Carex spp., Poa glauca).
2. Sequences of species were similar to the classical model of succession. Bare rock and xeric lichens were positioned at one extreme, with herbs and shrubs at the other.
3. Both axes could be related to soil depth. The variable "depth" was positioned high on both axes.

The individual site sequences of species derived from weighted averaging were positively correlated with one another at $P < 0.05$ (Appendix 4.5). The combined site sequence (Fig. 4.2) was positively correlated with the predicted sequence (Appendix 4.5). Deviations from the predicted sequence were generally species of later seral stages, especially chamaephytes (Table 4.2).

Figure 4.1: First and second axes of a reciprocal averaging/weighted averaging hybrid ordination for species (frequency $\geq$ 10), samples, and physiography from three sites.
Species maxima were standardized to 100 (Gauch 1977).
Sum of percent eigenvalues for these two axis was 11.64%.
For key to species numbers, see Appendix 4.3.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depth
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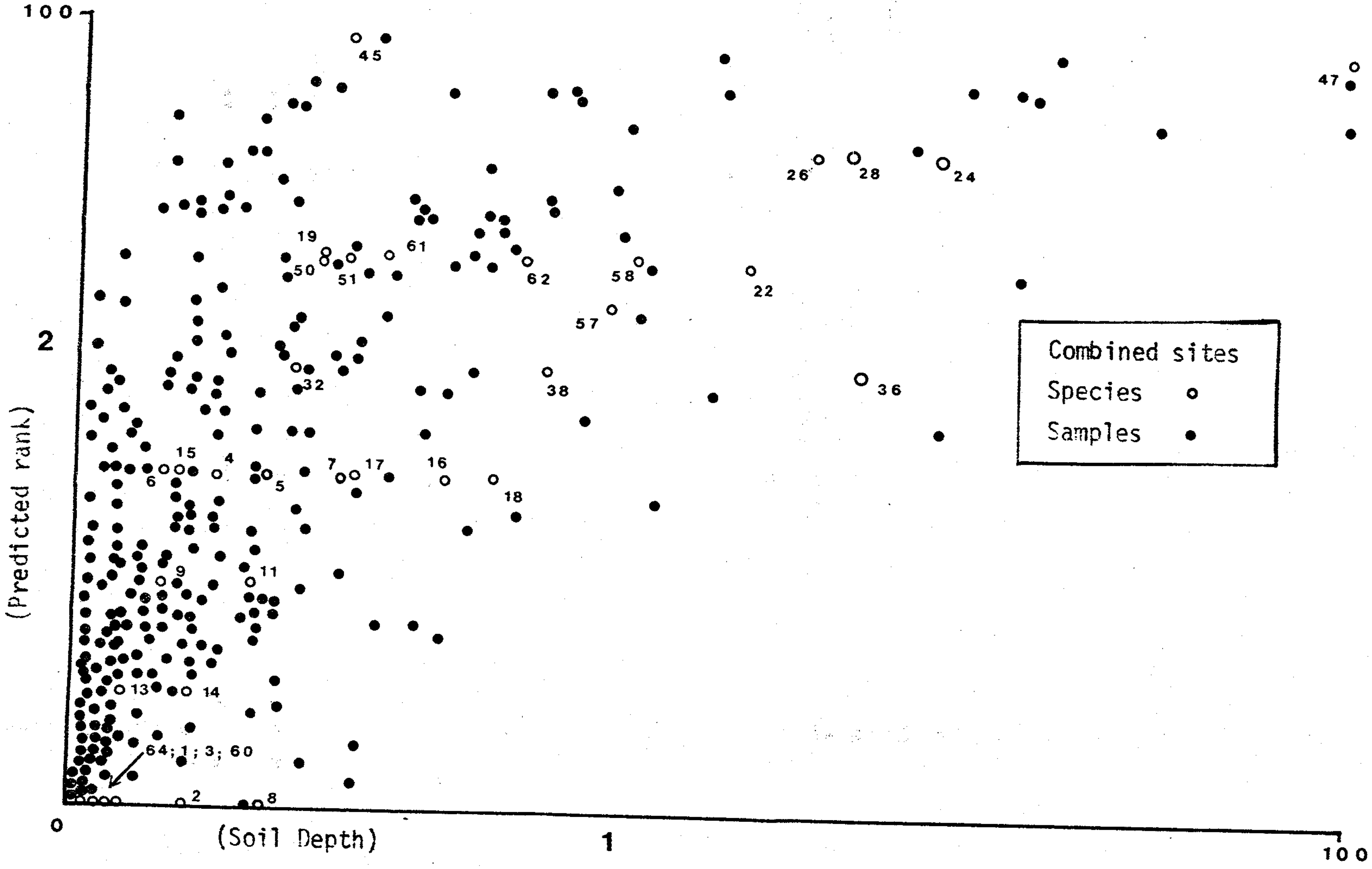
36
32
63
45
58
22
28
47
24
slope
elev
Combined sites
Species ○
Samples ●
Physiography ●

Figure 4.2: First and second axes of a weighted averaging ordination of species (frequency $\geq$ 10) and samples from three sites. Samples were weighted by soil depth (cm) on the first axis; species were weighted by predicted successional rank (see Table 4.1) on second axis. Species maxima standardized to 100 (Gauch 1977), key to species numbers, see Appendix 4.3.


100
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(Predicted rank)
0
(Soil Depth)
1
100
Combined sites
Species ○
Samples ●
45
47
26
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24
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50
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62
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38
36
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18
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11
13
14
64; 1; 3; 60
2
8

Table 4.2: Sequence of species from weighted averaging ordination, with corresponding rank from predicted sequence (0-7).

Crustose lichens	0
Physcia millegrana	0
Parmelia taractica	0
Bare rock	0
Grimmia unicolor	1
Cladina rangiferina	3
Cladonia pyxidata	2
Bryum pseudotriquetrum	3
Parmelia cumberlandica	0
Hedwigia ciliata	1
Peltigera rufescens	3
Tortula ruralis	2
Cladina mitis	3
Cladonia pocillum	0
Polygonum convolvulus	4
Parthenocissus inserta	5
Cladonia amaurocraea	3
Opuntia fragilis	5
Prunus pumila	7
Polytrichum juniperinum	3
Bare soil	5
Thuidium abietinum	3
Selaginella rupestris	3
Campanula rotundifolia	4
Saxifraga virginiensis	4
Solidago missouriensis	4.5
Poa glauca	5
Carex spp.	6
Silene antirrhina	6
Muhlenbergia racemosa	6
Crataegus spp.	7

Position of Opuntia fragilis

The clumps at Bird River contained the greatest number of old and new pads ($P < 0.05$, Table 4.3). In addition, pads at this site were the largest (Table 4.3, Appendix 4.6). Cactus vigour was not correlated with physiography or soil ($P > 0.05$, Appendix 4.7.).

The position of Opuntia fragilis at three sites differed ($P < 0.05$) in:

1. physiography (Table 4.3). The clumps at Big Whiteshell were located nearer the water level on a less steep slope than those at the other sites.
2. soil (Table 4.4). Soils under cacti at Big Whiteshell were lowest in pH, bulk density, and conductivity. Those at Bird River were highest in conductivity and available potassium (Appendix 4.8).
3. species richness (Table 4.5). Opuntia fragilis occurred with the greatest number of species at Bissett, and the least number at Bird River. It was found with more moss species at Bissett.

The cactus was most often found with none or one lichen species, zero to two moss species, and without vascular species (Table 4.5). It was positively associated with bare soil, Cladonia pyxidata, C. pocillum, Cladina rangiferina, Tortula ruralis, Saxifraga virginiensis, and Poa glauca; it was negatively associated with bare rock, Parmelia taractica, P. cumberlandica, Muhlenbergia racemosa, and Crataegus spp. (Appendix 4.9).

Table 4.3: Characteristics of colonies of *Opuntia fragilis* at three sites. Values are mean ± 1 s. Means joined by a horizontal bar are not significantly different ($P > 0.05$).

Characteristic	Site Big Whiteshell	 Bissett	 Bird	 Combined
Location:				
elevation (m)	4.79 ± 1.91	5.66 ± 1.46	5.85 ± 0.66	5.20 ± 1.72
slope	0.22 ± 0.09	0.40 ± 0.09	0.43 ± 0.07	0.30 ± 0.13
Colony:				
# new pads	103.51 ± 129.74	64.20 ± 54.03	210.81 ± 134.89	104.6 ± 0.11
total # pads	158.97 ± 191.63	143.12 ± 137.08	440.81 ± 277.20	189.60 ± 210.99
Pads:				
Length (cm)	2.36 ± 0.67	2.31 ± 0.56	3.06 ± 0.78	2.34 ± 0.53
Width (cm)	1.30 ± 0.30	1.35 ± 0.27	1.36 ± 0.30	1.29 ± 0.25
Depth (cm)	0.63 ± 0.14	0.65 ± 0.11	0.79 ± 0.17	0.66 ± 0.11
Fresh Weight (g)	1.25 ± 0.64	1.56 ± 0.70	2.09 ± 1.02	1.61 ± 0.80
Biomass (g) (dry weight)	0.21 ± 0.09	0.25 ± 0.10	0.27 ± 0.11	0.26 ± 0.11

Table 4.4: Soil properties of cactus colonies at three sites. Values are mean ± 1 s. Means joined by a horizontal bar are not significantly different ($P > 0.05$).

	Site			
Soil Property	Big Whiteshell	Bissett	Bird	Combined
Depth (cm)	2.01 ± 1.98	2.15 ± 1.62	2.25 ± 1.77	2.09 ± 1.84
pH	4.82 ± 0.50	6.00 ± 0.49	6.01 ± 0.37	5.34 ± 0.76
Conductivity (mmhos/cm)	0.16 ± 0.09	0.25 ± 0.12	0.34 ± 0.10	0.21 ± 0.12
% Moisture	7.51 ± 5.86	39.38 ± 22.28	48.69 ± 16.45	22.99 ± 22.65
% Organic Matter	47.23 ± 13.59	35.24 ± 6.01	36.13 ± 11.07	42.00 ± 12.73
Bulk density (g/ml)	0.36 ± 0.08	0.44 ± 0.05	0.41 ± 0.04	0.39 ± 0.08
Available phosphorus (kg/ha)	21.35 ± 21.36	7.26 ± 2.80	13.19 ± 4.04	15.74 ± 17.21
Available potassium (kg/ha)	7.21 ± 3.45	7.25 ± 1.90	9.71 ± 1.54	7.52 ± 2.95

Table 4.5: Comparison of species richness in individual 0.33m samples. Samples were selected to contain *Opuntia fragilis*, which is included as a vascular species below. Values are sample size (n), mean ± 1 standard deviation ($\bar{x}$ ± 1 *s*), and mode (most frequently occurring number).

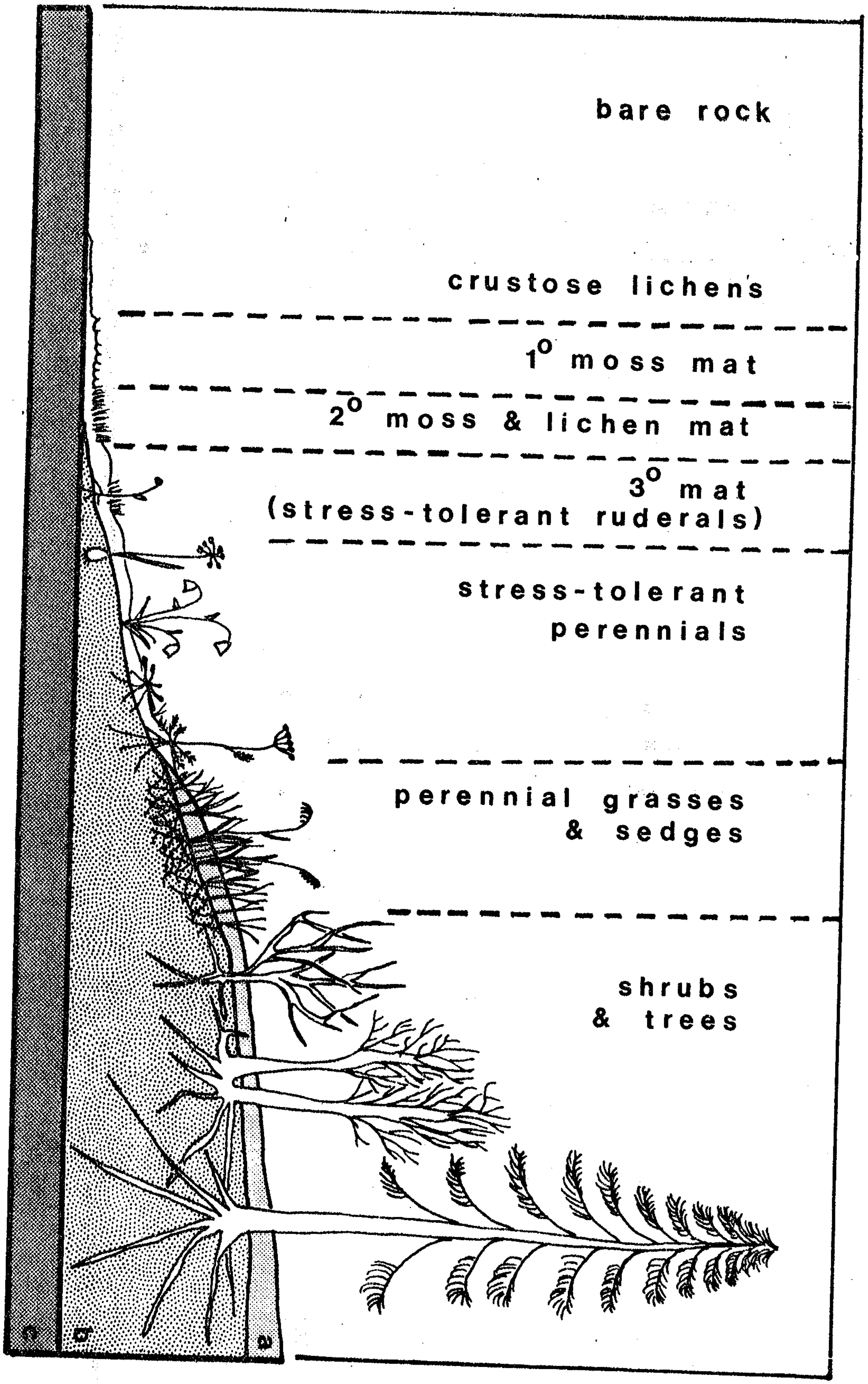
Plant Group	Site			
	Bissett	Bird River	Big Whiteshell	Combined
Moss				
$\bar{x}$ ± 1 *s*	2.20 ± 0.79	0.94 + 0.56	0.69 + 0.73	1.39 ± 1.03
m	2	1	0	2
Lichen				
$\bar{x}$ ± 1 *s*	0.67 ± 0.67	0.65 ± 0.99	1.31 ± 1.06	0.93 ± 0.95
m	0, 1	0	1	0
Vascular				
$\bar{x}$ ± 1 *s*	1.56 ± 0.86	1.24 ± 0.56	1.54 ± 0.85	1.50 ± 0.82
m	1	1	1	1
Combined				
$\bar{x}$ ± 1 *s*	3.72 ± 2.01	2.82 ± 1.07	3.79 ± 0.78	3.63 ± 1.51
m	4	2	3	3
n	54	17	52	123

Discussion

Successional Sequence on Outcrops

Description of Sequence on Manitoban outcrops. The earliest pioneer species were crustose lichens and low foliose and fruticose lichens such as *Parmelia taractica* (Fig. 4.3). The "primary moss mat", composed of *Grimmia unicolor*, *G. apocarpa*, and *Hedwigia ciliata*, was the true initiator of soil formation because it (1) colonized bare rock or pioneer lichen mats equally well, (2) produced more litter, and (3) trapped soil particles more effectively than crustose lichens. The deepest litter was invaded by a "secondary mat" of mosses (e.g. *Tortula ruralis*) and lichens (e.g. *Cladonia amaurocraea*), which increased the accumulation of micro-litter and inorganic particles. Soils > 1cm deep were colonized by a "tertiary mat" of clumped, robust mosses (e.g. *Polytrichum juniperinum*, *Thuidium abietinum*) and occasionally *Selaginella rupestris*. The pioneer lichen mat and "primary moss mat" were presumably eliminated by shading, burial, and seepage. Stress-tolerant ruderals, such as *Draba nemorosa*, were components of the secondary and tertiary stages. Their scant aerial biomass was lost from the mat by erosion, and the contribution of their root biomass to soil formation was negligible (McVaugh 1943). The next seral stage was composed of stress-tolerant perennials, which colonized soils of various depths but persisted only on deeper deposits such as in crevices or depressions. These species were low, spreading, and anchored litter and soil. The "real sod builders" (Hinds 1842) were perennial grasses which invaded deeper soil deposits. Their dense swards contributed to rapid

Figure 4.3: Successional sequence on rock outcrops in south-eastern Manitoba.


bare rock
crustose lichens
1° moss mat
2° moss & lichen mat
3° mat
(stress-tolerant ruderals)
stress-tolerant perennials
perennial grasses & sedges
shrubs & trees
c
b
a

detritus accumulation and eliminated previous stages, presumably by competition. The density of these stands occasionally (as at Bissett) prevented invasion by subsequent stages. The final stage in the successional sequence was composed of chamaephytes (e.g. *Crataegus* spp.) and stunted phanerophytes (e.g. *Populus tremuloides*) on soils > 6cm deep. Even the most sparse canopy contributed to litter accumulation and presumably reduced drying of the substrate by virtue of its shade.

Variations in sequence among sites. The initial stages of the successional sequence:

bare rock ----------> *Hedwigia* ---> *Tortula ruralis*
crustose lichens *ciliata* and *Opuntia*

were identical at all three sites. Presumably these species were consistent because they produce dust propagules (e.g. spores), hence are not dispersal limited, and/or are xerophytes. Variation in subsequent stages was attributed to:

1. *Availability of propagules*. Localized species which filled similar positions in the ordination sequence at different sites were presumably dispersal limited. *Polygonum douglasii* (Big Whiteshell) occupied a position similar to that of *Muhlenbergia racemosa* (Bird River). The chamaephyte position was filled by *Juniperus horizontalis* at Bissett, and by *Prunus virginiana*, *P. pensylvanica*, and *Crataegus* spp. at Bird River.
2. *Relative proportions of mesic and xeric species*. Potential colonizers from mesic habitats are more numerous than those adapted to xeric habitats, hence there is a greater chance of variation in more mesic seral stages than in xeric ones.

3. Extent of successional development. The Bird River contained extensive grass and chamaephyte/phanerophyte stages. The Bissett site was intermediate; development had reached the stress-tolerant perennial stage, with a few patches of perennial grass and one chamaephyte. The Big Whiteshell outcrop contained "secondary" and "tertiary" mats with stress-tolerant perennials and few patches of perennial grass.
4. Sampling technique. The location of shrub canopy was not always related to the depth of soil beneath it, as aerial cover, not rooted cover, was measured. The low positions of Prunus virginianum, P. pensylvanica, and Populus tremuloides in the weighted averaging ordination were due to branches which extended over bare rock and pioneer lichens.

Comparison of observed sequence with classical model. The successional sequence proposed for outcrops in southeastern Manitoba was similar to those observed by other workers in North America, and differed only slightly from the classical model of succession on bare rock.

1. Classical model. Clements (1963) proposed a concentric ring model of succession, in which bare rock was first colonized by crustose lichens. As the mechanical action of these lichens weathered the rock (Fry 1927), soil particles collected in the roughened surface. Foliose lichens invaded the deepest deposits at the centre, trapping more debris until fruticose lichens and xerophytic mosses invaded. The patch of vegetation continued to spread outward in concentric zones. Annual, biennial, and perennial herbs and forbs invaded the centre in turn.

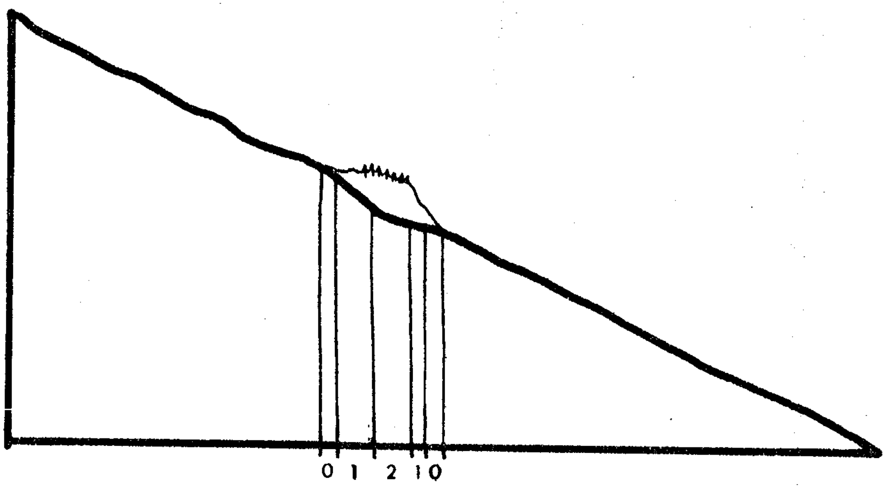
Eventually the humidity and protection afforded by the vegetation allowed the development of a thick mantle of soil, supporting a climax (mesic) forest.

This pattern of vegetation development on flat smooth outcrops occurs throughout North America, and has been described by Oosting and Anderson (1939), McVaugh (1943), and Winterringer and Vestal (1956). It can be seen in Whiteshell Provincial Park, Manitoba.

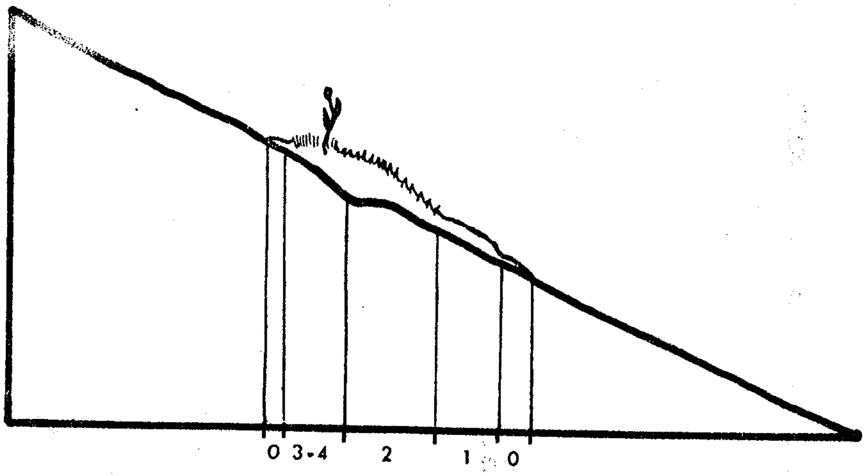
2. Deviation from the classical model. The discontinuous vegetation on outcrops suggests that deviation from Clements' model is not uncommon. On the Manitoban outcrops, four main deviations from the classical model were primarily due to physiography and disturbance:

(a) Pattern of spread. On the Manitoban outcrops, the pattern of vegetation was elongated or skewed rather than concentric. Colonization along soil-trapping cracks was much more extensive than lateral spread. Slope also skewed the pattern of spread. Eroded soil collected at the upper margin of moss mats and supported later seral stages, while initial colonizers advanced the lower edge (Fig. 4.4). Oosting and Anderson (1937) suggested that progression on the lower edge was accelerated by protection from erosion, and by prolonged moisture supply (seepage). The advancing edge therefore supported loosely attached secondary and even tertiary mat species, rather than primary mats which are intolerant of seepage. On smooth slopes, the skewed patches, anchored to the rock surface by moss rhizoids, were readily eroded. They rarely developed past the "stess-tolerant perennial" stage.

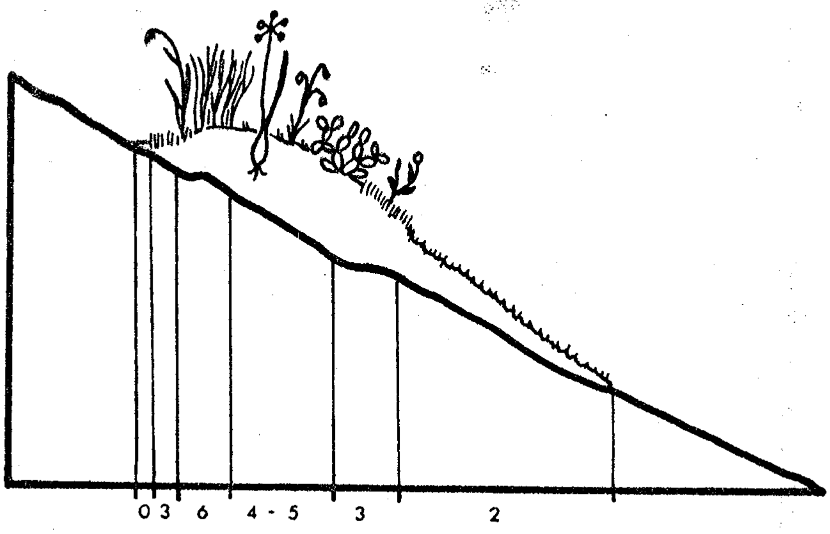
Figure 4.4: Three stages in the development (A through C) of a skewed vegetation mat on a rock slope. Numbers represent seral stages (see Table 4.1).
0 = pioneer lichens/bare rock,
1 = primary moss mat,
2 = secondary mat,
3 = tertiary mat,
4 = stress-tolerant ruderals,
5 = stress-tolerant perennials,
6 = perennial grasses and sedges.



A



B



C

(b) Reversal, prolongation of, or arrest at certain stages. The three Manitoban sites appeared to have reached different seral stages. In addition, a discontinuous mosaic of various stages occurred on individual outcrops. Inhibition of succession appeared to result from removal of soil or prevention of accumulation, which were related to slope, surface features, and substrate disturbance. Soil deposits, perhaps loosened by frost-leaving, were washed downhill by spring melt and summer rain. During the summer, bare dry soil was removed by wind. Eroded mats and soil often reached the river or lake, so were lost from the outcrop. Similar conditions were described elsewhere in North America by Whitehouse (1933) and McVaugh (1943). Soil erosion was further accelerated by the high temperatures and resulting dessication on south-facing slopes (Keever et al. 1951).

Minor disturbance may arrest succession, e.g. portage trails were devoid of vegetation. On very smooth steep slopes, where soil deposits are repeatedly eroded, bare rock or lichen communities formed a "pioneer equilibrium" (sensu Oosting and Anderson 1939). Extreme disturbance can reverse succession. In summer, dry moss and lichen mats are susceptible to fire, which often removes the shallow organic soils as well as vegetation (Kelsall et al. 1977). Remaining mineral soil and ash are frequently eroded, hence the outcrop is returned to bare rock.

(c) Acceleration of sequence. Acceleration, i.e. telescoping or elimination of early seral stages, occurred in seepage areas, crevices, and along the forest-outcrop ecotone. The effect of seepage was illustrated in the development of the lower edge of the skewed mat (Fig. 4.4).

Irregularities in the rock, which accelerated soil accumulation, also increased water retention. Pioneer and primary mat species were absent, presumably due to their intolerance of prolonged moisture (McVaugh 1943). Initial colonizers were loosely attached secondary and tertiary mats, and occasionally Opuntia fragilis. Acceleration of this kind was often later arrested by factors which limited soil development. At the Bird River site, a seedling of Pinus banksiana in approximately eight cm of soil was stunted by restricted root space and extreme fluctuations in soil moisture. Similar observations have been made elsewhere by Whitehouse (1933), McVaugh (1943), and Winterringer and Vestal (1956).

The forest-outcrop ecotone, where the soil was continuous with that under the forest canopy, was more mesic than the outcrop. As soil accumulated along the edge, some of the mesic forest vegetation invaded by means of rhizomes but was unable to extend onto the rock surface. Pioneer and primary mat species were absent, presumably due to shading and seepage. Hence the later, mesic, seral stages slowly extended over the rock.

(d) Discontinuity of vegetation. The rock-vegetation mosaic was attributable to different rates of succession at different points, i.e. (b) and (c) above, caused by rock surface features. On smooth steep surfaces, a "pioneer equilibrium" was maintained. Crevices, cracks, and depressions accelerated soil development and supported later seral stages. The scale of the mosaic varied according to the scale of rock surface features. Hence the samples containing one or two mesic species (Fig. 4.1) were partly due to a vegetation scale greater than 0.33m (c.f. Mueller-Dombois and Ellenberg 1976).

Position of *Opuntia fragilis* in the Sequence

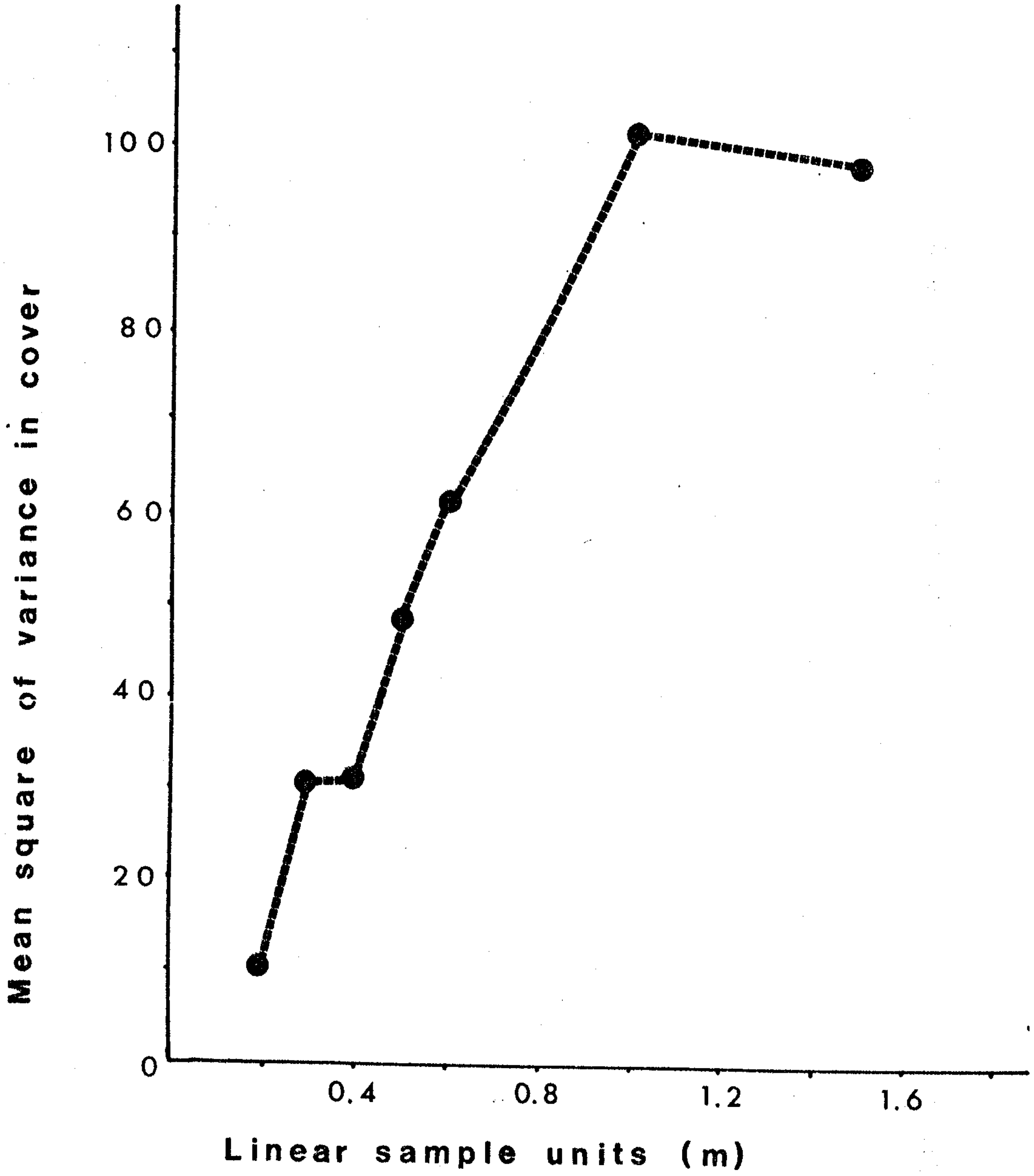
Opuntia fragilis occupied an earlier position in the successional sequence than predicted. It was not significantly associated with other stress-tolerant perennials. It was positively associated with bare soil, *Tortula ruralis*, *Cladonia pocillum*, *C. pyxidata*, *Cladina rangiferina*, and *Saxifraga virginiensis*. It was negatively associated with the initial stages of the sequence (e.g. bare rock, *Parmelia taractica*, and *P. cumberlandica*) and with later stages (*Crataegus* spp. and *Muhlenbergia racemosa*). This seral placement of *O. fragilis* was further supported by the finding that it was usually the only vascular species in a mixture of one or two moss and none or one lichen species in the 0.33m linear sample units. *O. fragilis* occurred at a mean soil depth of 2.09 ± 1.84 cm. Its position in the sequence may be attributed to its aerial perennating organs, which do not require a soil cover. The ecological position of *O. fragilis* could be further described by its physiography:

(location) 5.20 ± 1.72 m above water, (slope) 0.30 ± 0.13. Other soil features scarcely differed from those found on other outcrops in southeastern Manitoba (see Chapter II), i.e. soils were highly organic with low bulk density and low pH. Pad number was probably attributable to the length of time since their colonization and amount of disturbance. Pad number may be used as an indicator of the longevity of the *Opuntia* seral stage, i.e. the large colonies at Bird River are an example of a site in which the *Opuntia* seral stage has been prolonged.

Conclusions

The successional sequence on three geographically diverse outcrops in southeastern Manitoba is very similar in its initial stages and is generally consistent with the classical model described by Clements (1963), as well as outcrop succession described by other workers in North America. Succession can be halted, reversed, slowed, or accelerated on different parts of a single outcrop, by any factors which influence the rate of accumulation of soil, i.e. slope, aspect, rock surface features, and disturbance. Variation in these factors within a single outcrop results in a mosaic of bare rock and vegetation patches. Each of the latter represents a group of seral stages.

Opuntia fragilis occupies shallow soils with loosely attached secondary (occasionally tertiary) mat species, especially *Tortula ruralis*. The prolongation of succession on the outcrops suggests that the position occupied by *O. fragilis* has been available for a long time, and likely will be available indefinitely in southeastern Manitoba.



Appendix 4.1: Scales of vegetation cover using maximum mean square technique (Kershaw 1973, Mueller-Dombois and Ellenberg 1974). Peaks at 0.33m and 1.0m indicated that two scales of vegetation existed on the outcrop.

Appendix 4.2: Use of Ordination

Ordination is a trend-seeking technique particularly valuable in the initial stages of a study. Gittins (1969) stated, "The aim of analysis is to reveal precisely those relationships between plants and environment which are most likely to repay closer investigation." In ordination, multivariate data points are arranged along one or more axes by a selected statistical procedure. There are two major approaches to ordination (Gauch 1977):

1. It may be used as a mathematical tool to reduce the dimensionality of a data structure for inspection. These are termed "taxometric ordinations", or
2. It may be used to relate samples and species to environmental gradients, thereby relating patterns in communities to patterns in environmental factors. This is called "ecological ordination", and forms the main focus of this study.

Four techniques are commonly used: principal components analysis (PCA), polar ordination (PO), reciprocal averaging (RA), and weighted averaging (WA). Their effective use depends on the assumptions, strengths and weaknesses of the technique, taking into account the dataset properties. The general attributes of these techniques are from Gauch (1977).

Appendix 4.2:

PCA and RA are mathematically objective, and both are eigen analysis techniques, i.e. the variance in the data explained by each axis is expressed as an eigenvalue in the form of a percentage of total variation. PCA is based on assumptions of linearity which do not hold in normally distributed data. RA may provide an excellent first axis, but is subject to curvilinear distortion of subsequent axes.

WA and PO require a priori decisions, so may be very subjective. The statistician selects the extremes (or endpoints) of the gradient for PO, and positions (or weights) of species (or samples) in WA. There is no statistic in either technique to express the proportion of variance explained by the ordination. Both techniques are subject to less distortion on subsequent axes than RA and PCA, and are very useful when some knowledge of the system has been acquired.

Gauch (1977) pointed out that "ordination performance is strongly affected by data set properties, including beta diversity (i.e. heterogeneity), disjunction versus continuity, noise level (i.e. random variation), and the number of environmental gradients which influence the intrinsic dimensionality of the data matrix." It is important to reduce the variation due to intrinsic differences in order to clarify the ecological differences that are of interest.

Appendix 4.2:

First, floristic and environmental data must be ordinated separately. Second, the data in each data set must be commensurate. When variables have different scales of measure, transformation must be used to standardize the scales. (A thorough discussion of transformation techniques and their implications is found in Noy Meir *et al.*, 1975).

Gauch (1977) suggested a technique for combining the results of ordination of two data sets when there is a third in common. He termed the following technique a RA/WA hybrid. First the data set of primary interest is ordinated by RA and the best two axes chosen. The RA scores of the common data set are then extracted and used to weigh the same set in the second ordination. WA is performed, resulting in placement of the third set on a common pair of axes with the first and second sets. As Gittins (1969) showed, the contribution of the variables from the third set to the initial ordination can be determined by their position on the axes. This hybrid technique was found to be useful in my study.

Appendix 4.3: Species encountered on 15 transects. Vascular plants fide Scoggan (1978); bryophytes fide Crum (1976), verified by R.R. Ireland; lichens verified by P. Wong.

	I. Lichens	Bissett	Bird	Big W.
	PHYSCIACEAE			
1.	*Physcia millegrana* Degel.			X
	PARMELIACEAE			
2.	*Parmelia cumberlandia* (Gyeln.) Hale	X	X	
3.	*P. taractica* Kremp.	X	X	X
	PELTIGERACEAE			
4.	*Peltigera rufescens* (Weiss) Humb.		X	X
	CLADONIACEAE			
5.	*Cladina mitis* (Sandst.) Hale & W. Culb.	X		
6.	*C. rangiferina* (L.) Nyl.		X	X
7.	*Cladonia amaurocraea* (Florke) Schaer.		X	X
8.	*C. pocillum* (Ach.) O. Rich.	X		X
9.	*C. pyxidata* (L.) Hoffm.	X	X	X
64.	CRUSTOSE SPECIES	X	X	X
	II. BRYOPHYTES			
	DITRICHACEAE			
10.	*Ceratodon purpureus* (Hedw.) Brid.	X	X	
	POTTIACEAE			
11.	*Tortula ruralis* (Hedw.) Gtrtn., Meyer, & Scherb.	X	X	X
	GRIMMIACEAE			
12.	*Grimmia apocarpa* Hedw.	X		
13.	*G. unicolor* Hook. *ex* Grev.	X		X
	HEDWIGIACEAE			
14.	*Hedwigia ciliata* (Hedwig) P. Beauv.	X	X	X
	BRYACEAE			
15.	*Bryum pseudotriquetrum* (Hedw.) Gtrtn., Meyer, & Scherb.			X
	LESKEACEAE			
16.	*Thuidium abietinum* (Hedw.) BSG	X	X	
	POLYTRICHACEAE			
17.	*Polytrichum juniperinum* (Hedw.)	X	X	X

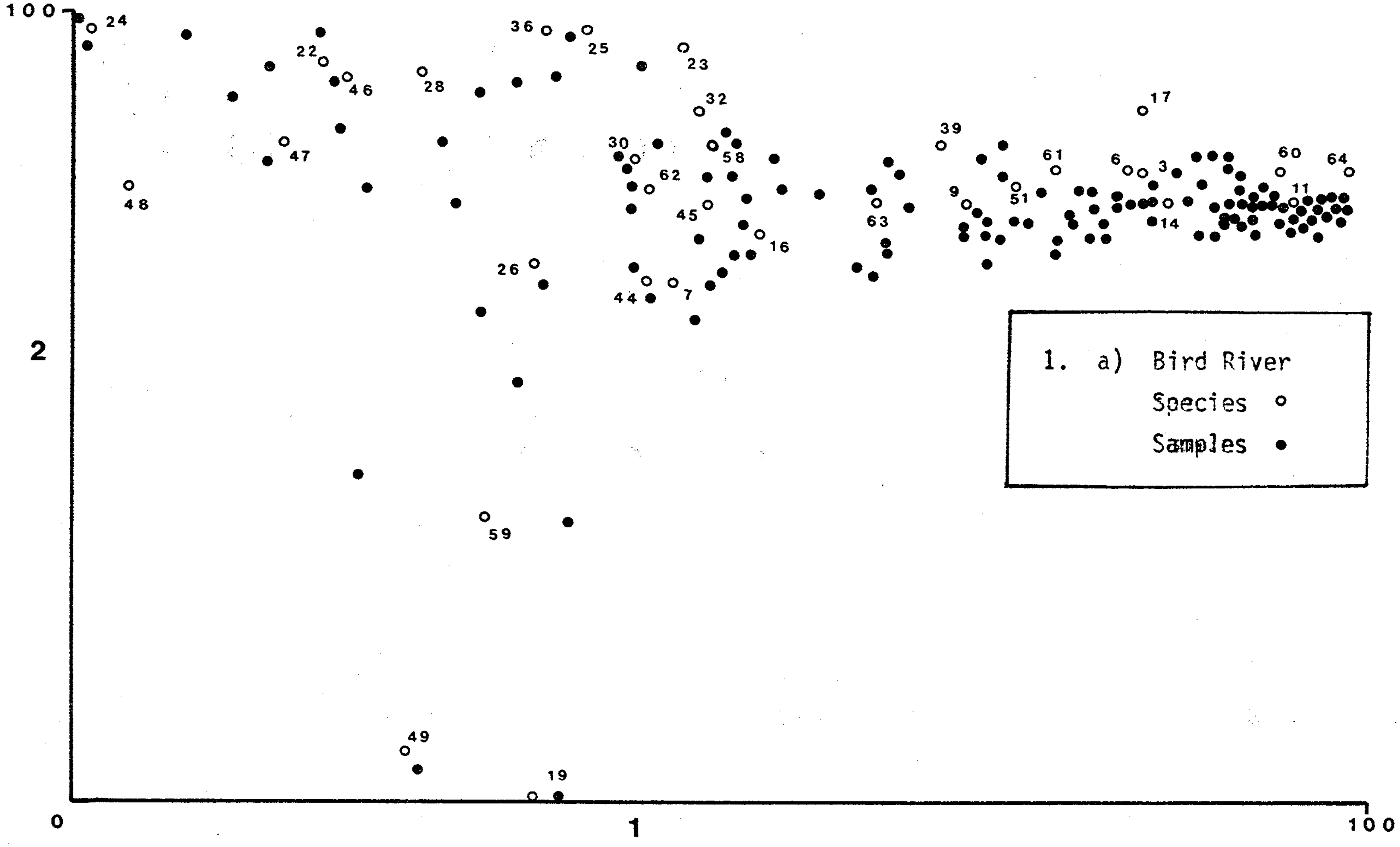
		Bissett	Bird	Big W.
	III. FERNS & FERN ALLIES			
	SELAGINELLACEAE			
18.	*Selaginella rupestris* (L.) Spring	X	X	
	POLYPODIACEAE			
19.	*Woodsia ilvensis* (L.) R. Br.	X	X	
	IV. CONIFERS			
	PINACEAE			
20.	*Juniperus communis* L.	X		
21.	*J. horizontalis* Moench	X		
	V. ANGIOSPERMS			
	GRAMINEAE			
22.	*Agropyron trachycaulon* (Link) Malte var. *novae-angliae* (Scribn.) Fern.	X	X	X
23.	*Andropogon gerardi* Vit.		X	
24.	*Muhlenbergia racemosa* (Michx) BSP.		X	
65.	Unidentified grass	X		
25.	*Panicum capillare* L.		X	
26.	*Poa glauca* Vahl	X		
	CYPERACEAE			
27.	*Carex scoparia* Schk.			X
28.	*Carex* sp.		X	
	LILIACEAE			
29.	*Allium stellatum* Fraser	X	X	
	SALICACEAE			
30.	*Populus tremuloides* Michx.		X	
	BETULACEAE			
31.	*Corylus cornuta* Marsh.			X
	POLYGONACEAE			
32.	*Polygonum convolvulus* L.		X	X
33.	*P. douglasii* Greene	X		
	PORTULACACEAE			
34.	*Portulaca oleracea* L.	X		
	CARYOPHYLLACEAE			
35.	*Cerastium nutans* Raf.			X
36.	*Silene antirrhina* L.	X	X	X

		Bissett	Bird	Big W.
	RANUNCULACEAE			
37.	*Aquilegia canadensis* L.	X		
	SAXIFRAGACEAE			
38.	*Saxifraga virginiensis* Michx.	X		
39.	*Ribes oxyacanthoides* L.		X	X
	ROSACEAE			
40.	*Rosa* sp.			X
41.	*Potentilla norvegica* L.	X		
42.	*P. rivalis* Nutt. var. *millegrana* (Engelm.) Wats.	X		X
43.	*Rubus idaeus* L.			X
44.	*Prunus pensylvanica* L.		X	
45.	*P. pumila* L.		X	
46.	*P. virginiana* L.		X	
47.	*Crataegus* spp.		X	
	LEGUMINOSAE			
48.	*Vicia americana* Muhl.		X	
	GERANIACEAE			
49.	*Geranium bicknellii* Britt.		X	
	VITACEAE			
50.	*Parthenocissus inserta* (Kerner) K. Fritsch	X		
	CACTACEAE			
51.	*Opuntia fragilis* (Nutt.) Haw.	X	X	X
	ERICACEAE			
52.	*Arctostaphylos uva-ursi* (L.) Spreng.		X	
	APOCYNACEAE			
53.	*Apocynum androsaemifolium* L.		X	
	LABIATAE			
54.	*Agastache foeniculum* (Pursh) Ktze.	X		
	RUBIACEAE			
55.	*Galium boreale* L.	X	X	
	CAPRIFOLIACEAE			
56.	*Symphoricarpos albus* (L.) Blake		X	
	CAMPANULACEAE			
57.	*Campanula rotundifolia* L.	X	X	X
	COMPOSITAE			
58.	*Solidago* spp.		X	
59.	*Achillea millefolium* L.	X	X	
	VI. SUBSTRATES			
60.	Rock	X	X	X
61.	Soil	X	X	X
62.	Litter	X	X	X
63.	Wood	X	X	X

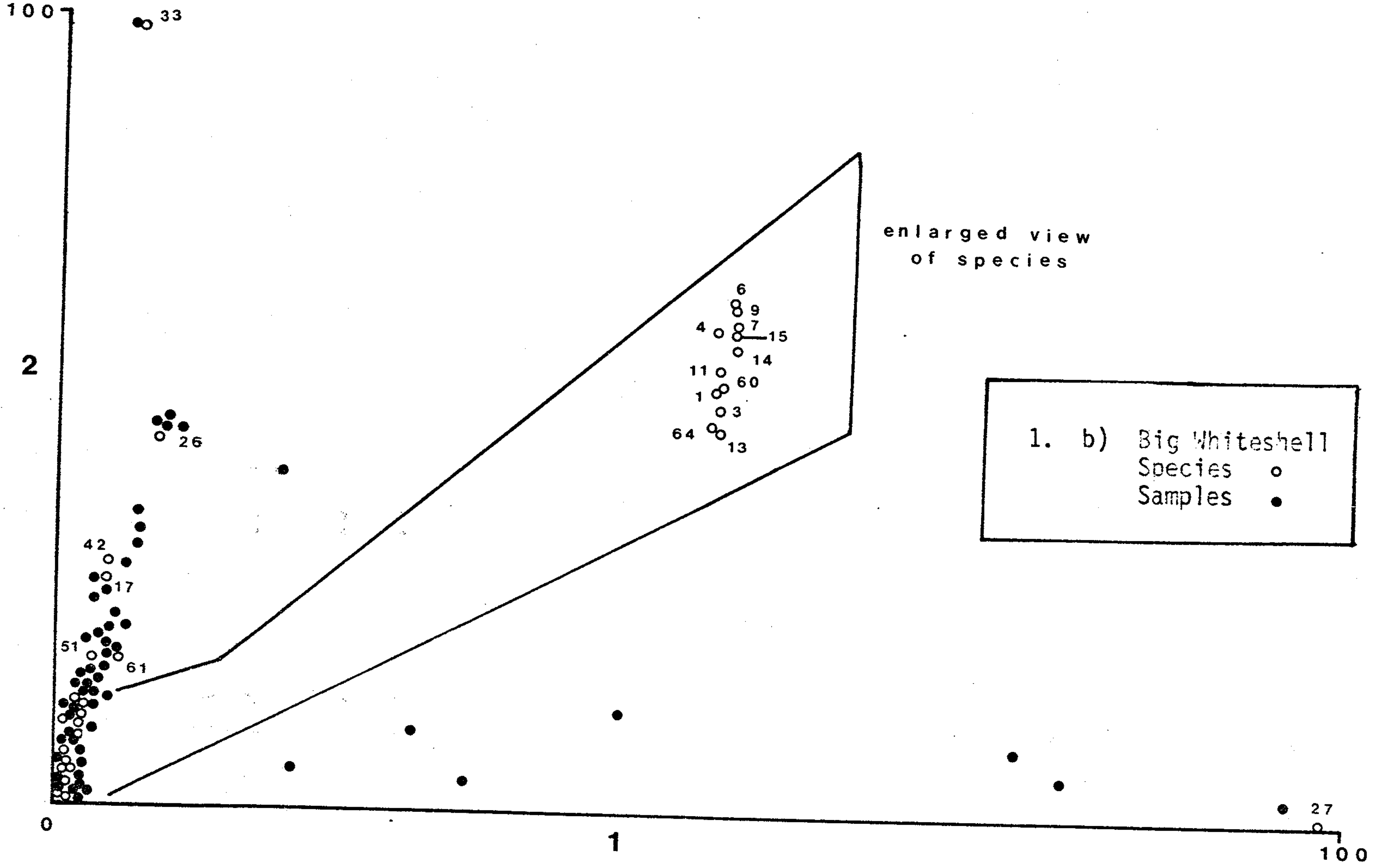
Appendix 4.4: Ordination diagrams for individual sites.

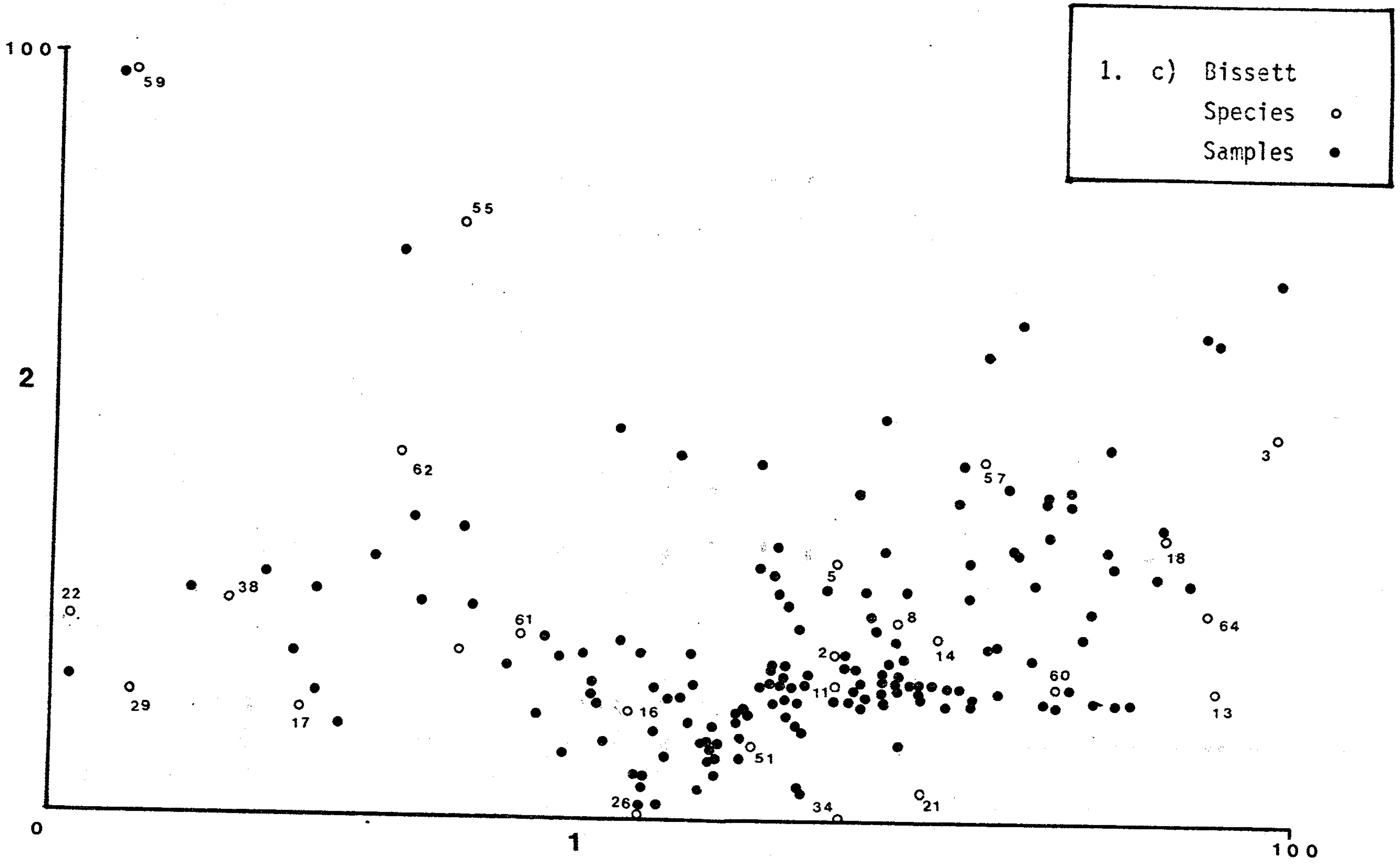
Maxima of species cover (frequency ≥ 4) were standardized to 100 (Gauch 1977). Key to species numbers in Appendix 4.3.

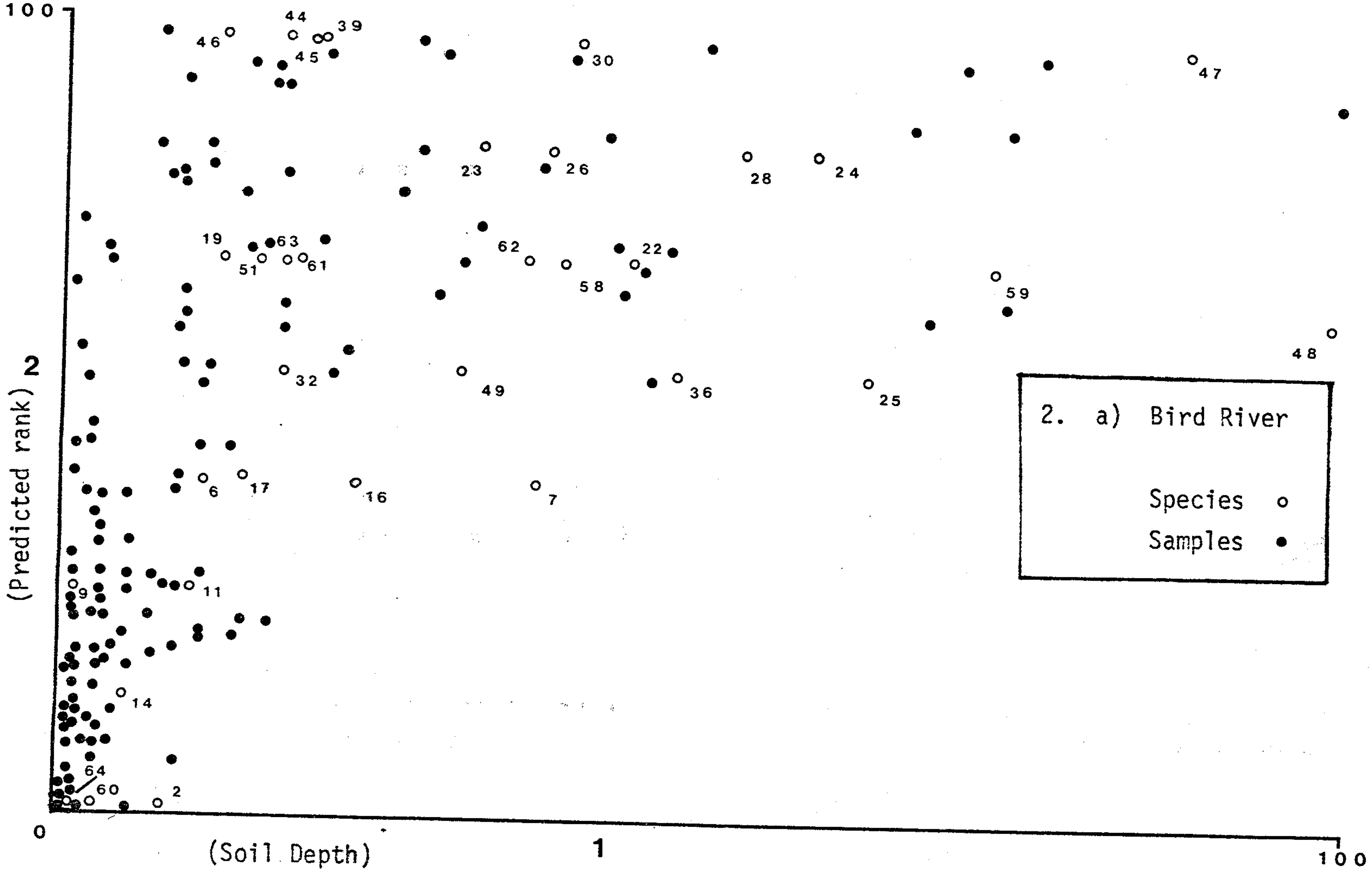
1. Reciprocal averaging, first two axes.
   a) Bird River; sum of % eigenvalues = 12.66%.
   b) Big Whiteshell; sum of % eigenvalues = 19.74%.
   c) Bissett; sum of % eigenvalues = 15.23%.
2. Weighted Averaging, first two axes. Samples were weighted by soil depth standardized to 100 on the first axis. Species were weighted by predicted successional rank (Table 4.1) on the second axis.
   a) Bird River.
   b) Big Whiteshell.
   c) Bissett.

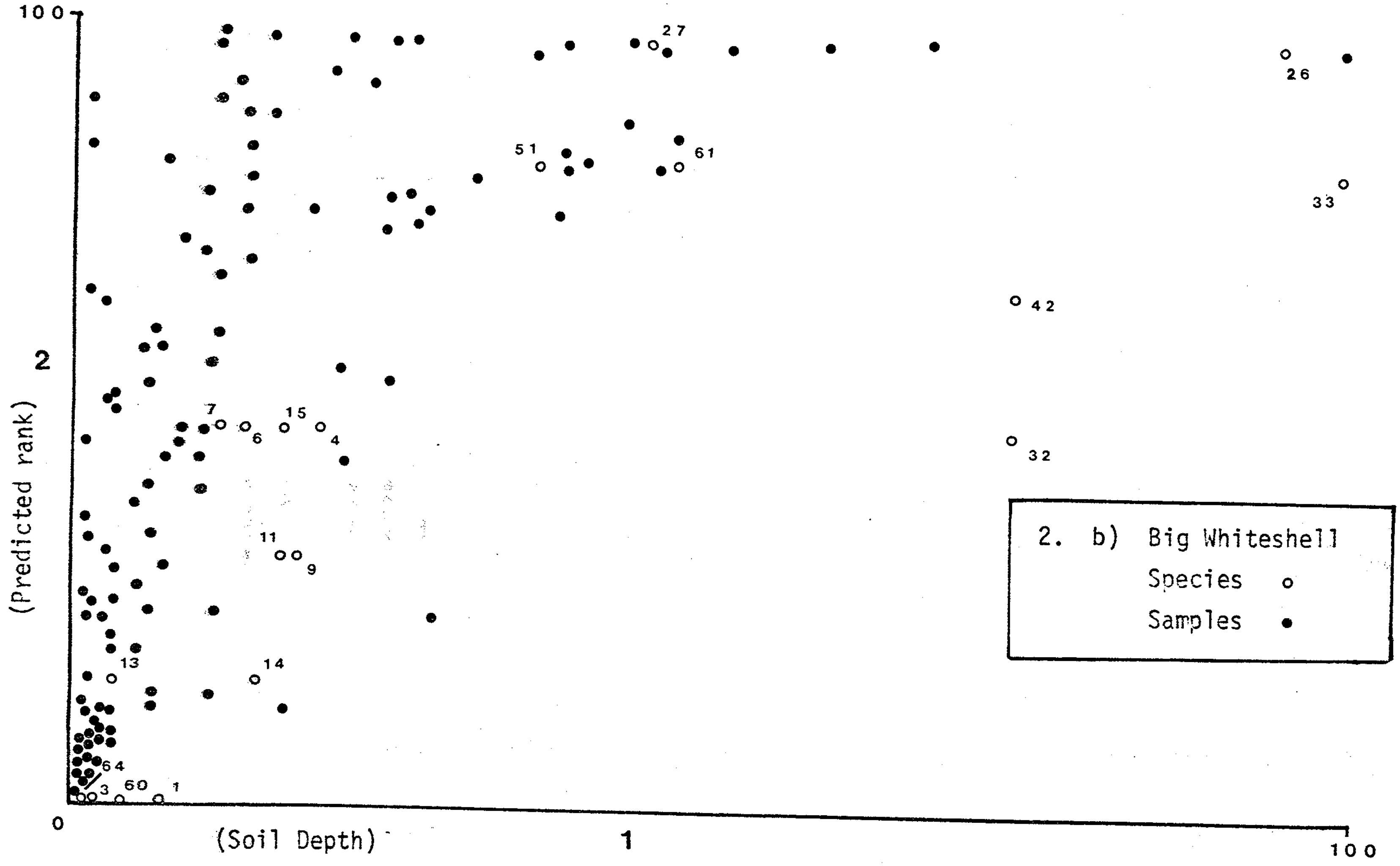


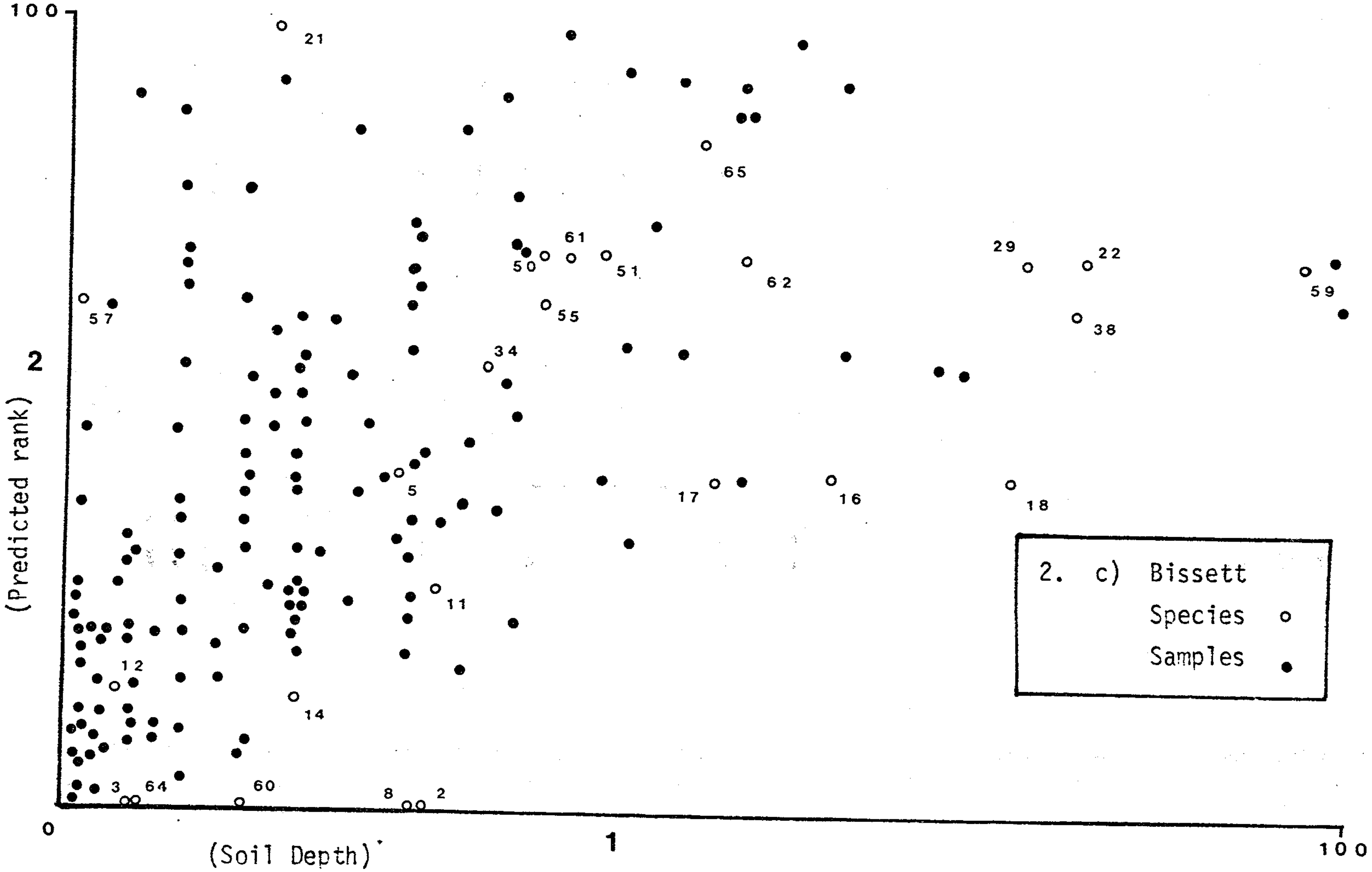
1. a) Bird River
Species ○
Samples ●
100
2
0
1
100
24
22
46
47
48
28
36
25
23
32
30
62
58
45
16
44
7
26
59
49
19
39
9
63
61
51
6
3
17
14
60
64
11


100
33
2
26
42
17
51
61
0
1
100
27
enlarged view of species
6
9
4
7
15
14
11
60
1
3
64
13
1. b) Big Whiteshell
Species ○
Samples ●


1. c) Bissett
Species ○
Samples ●
100
2
0
1
100
59
55
62
22
38
29
17
61
16
26
51
34
5
2
11
8
14
21
57
60
18
64
13
3


100
2
(Predicted rank)
0
(Soil Depth)
1
100
2. a) Bird River
Species ○
Samples ●
44
39
46
45
30
47
23
26
28
24
19
63
51
61
62
22
58
59
48
32
49
36
25
6
17
16
7
9
11
14
64
60
2


100
2
(Predicted rank)
0
(Soil Depth)
1
100
27
26
51
61
33
42
32
7
15
6
4
11
9
13
14
64
3
60
1
2. b) Big Whiteshell
Species ○
Samples ●


100
2
0
(Predicted rank)
1
100
(Soil Depth)
21
65
61
50
51
62
29
22
59
57
55
38
34
5
17
16
18
11
12
14
3
64
60
8
2
2. c) Bissett
Species ○
Samples ●

Appendix 4.5: Spearman's rank correlation coefficients for:

1. sequence obtained from weighted averaging versus predicted sequence (Table 4.1), and
2. sequences obtained by weighted averaging at three sites. Values are r_s; all values were highly significant at $P < 0.05$.

(1) Combined Sites	0.805

(2) Individual Sites

Site	Site		
	Bird River	Bissett	Big Whiteshell
Bird River	1.000	-	-
Bissett	0.960	1.000	-
Big Whiteshell	0.997	0.835	1.000

Appendix 4.6: One-way analysis of variance tables for physiographic and colony properties of three sites. * indicates significant difference among site means at P < 0.05.

Variable	Source of Variance	Degrees of Freedom	Sum of Squares	Mean Sum of Squares	F	
Elevation (m)	Cell means	2	217.79	108.90	76.36	*
	error	125	178.27	1.43		
Slope	Cell means	2	1.08	0.54	72.58	*
	error	125	0.93	0.01		
# New pads per colony	Cell means	2	226,682.3	113,341.2	9.04	*
	error	124	1,555,146.0	12,541.5		
Total # pads per colony	Cell means	2	1,113,903.6	556,951.8	15.81	*
	error	124	4,369,347.6	35,236.7		
Pad length (cm)	Cell means	2	74.31	37.16	93.83	*
	error	1285	508.87	0.40		
Pad width (cm)	Cell means	2	0.78	0.39	4.67	*
	error	1285	106.74	0.08		
Pad depth (cm)	Cell means	2	3.33	1.67	99.53	*
	error	1285	21.50	0.02		
Pad weight (g)	Cell means	2	87.66	43.83	83.32	*
	error	1285	675.91	0.53		
Pad biomass (dry weight)(g)	Cell means	2	0.55	0.28	27.40	*
	error	1285	12.91	0.01		

Appendix 4.7: Correlation matrix of cactus vigour versus environmental variables. None were significant (P > 0.05).

	Cactus Vigour						
Environmental Variables	Pad Length (mm)	Pad Width (mm)	Pad Depth (mm)	Pad Weight (gm)	Pad Dry Weight (gm)	# New Pads	Total # Pads
a) Soil							
pH	0.111	0.175	0.176	0.093	0.052	0.022	0.159
Conductivity	-0.021	0.134	-0.076	0.205	0.220	0.064	0.137
Available phosphorous	0.099	0.201	-0.108	0.300	0.334	0.229	0.125
Available potassium	-0.221	-0.183	-0.335	0.027	0.071	0.074	0.066
% Organic content	0.045	0.222	-0.021	0.105	0.116	0.123	0.211
% Moisture content	-0.202	0.226	-0.352	-0.054	0.018	-0.114	-0.157
b) Physiography							
Substrate depth	0.286	0.231	0.111	0.247	0.190	0.103	0.037
Slope	0.049	0.126	0.216	0.022	-0.001	-0.007	0.177
Height above water level	0.215	0.053	0.220	0.142	0.068	-0.245	-0.209
c) Species Diversity							
# Plant species present	0.038	0.087	-0.060	-0.048	-0.064	0.154	0.173
# Moss spp. present	-0.061	0.050	-0.064	-0.054	-0.044	0.101	0.226
# Lichen spp. present	-0.163	-0.217	-0.163	-0.157	-0.133	-0.052	-0.118
# Vascular spp. present	0.324	0.333	0.161	0.168	0.102	0.176	0.133

Appendix 4.8: One-way analysis of variance tables for soil properties at three sites. * indicates significance at $P < 0.05$, n.s. = not significant.

Variable	Source of Variance	SS	MS	df	F	
pH	Cell means	37.19	18.59	2	101.35	*
	error	16.69	0.18	91		
Conductivity	Cell means	0.26	0.13	2	12.90	*
	error	0.93	0.01	91		
Available Phosphorus	Cell means	11,366.98	5,683.49	2	9.32	*
	error	55,511.12	610.01	91		
Available Potassium	Cell means	34,932,224.00	17,466,112.00	2	7.57	*
	error	209,858.928.00	2,306,142.00	91		
% Moisture Content	Cell means	20.54	10.27	2	1.39	n.s.
	error	671.40	7.38	91		
% Organic Content	Cell means	0.16	0.08	2	0.009	n.s.
	error	777.71	8.55	91		
Bulk Density	Cell means	0.195	0.018	2	49.14	*
	error	0.248	0.002	125		
Depth	Cell means	0.30	0.15	2	0.04	n.s.
	error	435.40	3.48	125		

Appendix 4.9: Chi-square values calculated for occurrence of species with *Opuntia fragilis* in 0.33m segments of a transect. * indicates a significant association between the species and *O. fragilis* ($P < 0.05$).

Species	Calculated chi-square		Association
Bryum pseudotriquetrum	0.003		
Ceratium purpureum	0.009		
Grimmia unicolor	1.372		
Thuidium abietinum	1.306		
Grimmia apocarpa	0.009		
Hedwigia ciliata	0.424		
Polytrichum juniperinum	0.016		
Selaginella rupestris	0.000		
Tortula ruralis	27.020	*	Positive
Achillea millefolium	2.295		
Agastache foeniculum	0.241		
Agropyron trachycaulon	0.201		
Allium stellatum	0.027		
Andropogon gerardi	0.813		
Apocynum androsaemifolium	0.241		
Aquilegia canadensis	0.241		
Campanula rotundifolia	0.291		
Carex scoparius	0.181		
Cerastium nutans	2.201		
Corylus cornuta	0.192		
Crataegus spp.	5.092	*	Negative
Galium boreale	0.027		
Geranium bicknellii	0.481		
Juniperus communis	0.009		
J. horizontalis	0.036		
Panicum capillare	0.813		
Parthenocissus inserta	3.698		
Polygonum convolvulus	2.855		
P. douglasii	0.192		
Portulaca oleracea	0.540		
Potentilla rivalis	0.210		
P. norvegica	0.241		
Prunus virginiana	0.481		
P. pumila	0.857		
P. pensylvanica	0.181		
Ribes oxyacanthoides	0.210		
Rosa sp.	0.241		

Continued ...

Appendix 4.9, continued.

Species	Calculated chi-square		Association
Rubus idaeus	0.192		
Saxifraga virginiana	5.854	*	Positive
Silene antirrhina	0.046		
Solidago spp.	3.663		
Symphoricarpos alba	0.192		
Vicia americana	0.481		
Woodsia ilvensis	0.813		
Leaf litter	0.353		
Wood	1.403		
Bare soil	4.880	*	Positive
Bare rock	6.058	*	Negative
Cladonia amaurocraea	0.152		
C. pyxidata	15.620	*	Positive
C. pocillum	4.249	*	Positive
Cladina rangiferina	4.608	*	Positive
Crustose lichens	1.613		
Cladina mitis	3.663		
Muhlenbergia sp.	0.009		
Carex spp.	3.597		
Muhlenbergia racemosa	4.363	*	Negative
Parmelia taractica	4.956	*	Negative
Populus tremuloides	1.167		
Unknown grass species	4.424	*	Positive
Poa glauca	6.899	*	Positive
Parmelia cumberlandica	14.909	*	Negative
Physcia milligrana	0.997		
Peltigera rufescens	3.638		

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CHAPTER FIVE

Conclusions

1. Distribution and Habitat.

Opuntia fragilis occurs throughout the Boreal Forest Region of southeastern Manitoba, from Indian Bay (49°37'N, 95°12'W) to Bissett (51°02'N, 95°41'W). More northern colonies have been reported, but not verified. The seven colonies have been contained over 1000 pads each. This provided a source of propagules for further spread.

Cactus colonies were located in acidic, nutrient-poor organic soils in moss mats, on south-facing rock outcrops along waterways, 3-4m above water level. This habitat was more xeric than forest or north-facing habitats.

2. Restrictions on Distribution.

Pads were dispersed over short distances by geochory, and over longer distances by epizoochory and hydrochory. Their confinement to waterways suggested that hydrochory was the main dispersal mechanism.

Although pads could be dispersed to various boreal habitats, they became established only on south-facing outcrops. This suggested a requirement for high light intensity and temperature, or an inability to compete in more mesic habitats.

Once established on south-facing outcrops, colonies appeared to be able to maintain or increase their size over periods of at least twenty years, presumably unless destroyed by severe disturbance, e.g. fire.

The distribution of this species appeared to be restricted to availability of suitable habitats, and by dispersal mechanisms.

3. Position in Successional Sequence.

The sequence of vegetation on rock outcrops appeared to be a temporal continuum from bare rock to forest canopy. The continuum was often altered (temporally or spatially) by any factors which altered the rate of soil accumulation. Variation in aspect, slope, rock surface features, and disturbance resulted in a spatial mosaic of seral stages, caused by local acceleration, arrest, or reversal of succession.

Opuntia fragilis was positively associated with species in the secondary (occasionally tertiary) mat stages, e.g. *Tortula ruralis*, *Cladonia pyxidata*, *C. pocillum*, *Cladina rangiferina*, *Saxifraga virginiensis*, and bare soil. It occupied an earlier stage than the other stress-tolerant perennials, presumably due to its aerial perennating organs which did not require a soil cover.