Bur Oak (*Quercus macrocarpa* Michx.) in Riding Mountain National Park

By
Kim Wolfe

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

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

0-612-62869-8

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION

BUR OAK (*Quercus macrocarpa* Michx.) IN RIDING MOUNTAIN NATIONAL PARK

BY

KIM WOLFE

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirement of the degree

of

MASTER OF SCIENCE

THESIS RECORD SHEET

Page Numbers	**162**
NAME	**WOLFE, Kim** **Box 35** **Carman, Manitoba** **R0G 0J0**
Graduation Date	**October 2001**
Degree	**MASTER OF SCIENCE**

Title of Thesis (or Practicum)

BUR OAK (*Quercus macrocarpa* Michx.) IN RIDING MOUNTAIN NATIONAL PARK

Examiners (and their Departments):

Advisor:	**Dr. N. Kenkel**	**Department of Botany**
	Dr. B. Ford	**Department of Botany**
	Dr. S. McLachlan	**Department of Botany (Environmental Science Program)**
	Dr. W. Remphrey	**Department of Plant Science**

Budget #

Received **Copies 2** **Sent**

Approved	**JUNE 29, 2001**
Sent to Library	**SEPTEMBER 24, 2001**

ACKNOWLEDGMENTS

I would like to thank the following people who provided funding, advise, and support for this project.

Heritage Canada, Parks, provided funding for this project. Additional funding for summer help was provided by the Natural Sciences and Engineering Research Council (NSERC), and Manitoba Careerstart.

Wybo Vanderschuit, head vegetation warden for Riding Mountain National Park, is responsible for creating the project, which is greatly appreciated. I also acknowledge other RMNP staff, Terry Hoggins, Gord Pylypiuk, and Jacques Saquet for their advice and field assistance.

Advisory committee members Drs. B. Ford, S. McClaughlan, and B. Remphrey for advice and time spent on the thesis.

Field assistants Cathy Foster and Shaun Hermiston, provided field assistance. I am also grateful to Richard Caners for volunteering his time to assist in field work, and Dave Walker and Rod Lastra for technical assistance.

My family and friends who have provided the emotional support when I needed it the most. I thank Pam, for all our Friday afternoon meetings to unwind, and everyone in the lab for the always-interesting discussions. Finally, I wish to sincerely thank Kelly and my family, for their patience and unending support during my entire university career.

Most importantly, I thank my advisor, Dr. N.C. Kenkel, for his patient and productive teaching. I have learned valuable, practical skills while under his tutelage.

ABSTRACT

Little in known about the extensive *Quercus macrocarpa* stands occurring in Riding Mountain National Park (RMNP). The main topographical feature of the Park is the Manitoba Escarpment, which rises 300 m above the Manitoba Plain to the east. Several gorges, old beach ridges and outwash plains occur along the eastern slopes of the Escarpment. *Q. macrocarpa* stands occur as monodominant stands on these xeric sites, or in mixed stands on more mesic substrates. Baseline information including the population dynamics, floristic composition, community structure and vegetation-environment relationships of *Q. macrocarpa* stands was collected. A total of 191 sample plots were enumerated over two field seasons (1998-1999). Species abundance data and statistical analysis were used to classify the plots into three stand types based on a complex moisture gradient. Organic matter, exposure, percent sand, conductivity, and slope were also strong determinants of stand and community structure. Recruitment of *Q. macrocarpa* was highest in more open stands in xeric sites and lowest in closed stands due to low light conditions.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1
LITERATURE REVIEW

1.1 *Quercus macrocarpa* In A Regional Context

1.1.1 Boreal Mixedwood Ecoregion

Riding Mountain National Park occurs in the extreme eastern portion of the Canadian boreal mixedwood forest (**Fig. 1.1**). Although considered part of the boreal forest, the Park actually includes three major ecosystems: the northern boreal forest, the fescue grasslands, and the eastern deciduous forest. Aspen parkland vegetation is common in the western uplands, while *Q. macrocarpa* is most commonly encountered along the base of the Manitoba Escarpment. *Q. macrocarpa* may occur in pure stands in excessively drained sites, but it is also found in mixture with *Populus tremuloides*, *Fraxinus pennsylvanica*, *Acer negundo*, *Populus balsamifera* and *Ulmus americana*.

1.1.2 Climate

The northwestern range of *Q. macrocarpa* includes an area encompassing eastern Saskatchewan, southern Manitoba, and the Dakotas. This area is typified by a continental, subhumid climate with extreme daily and annual temperature fluctuations, low humidity, erratic precipitation and high winds (Killingbeck & Wali 1978). The average annual precipitation may be as low as 380 mm (Johnson 1990) with mean monthly temperatures varying from 20°C to -20°C. This extreme climate of very cold winters, relatively short warm summers, and low precipitation results in soil moisture deficits in late summer (Ritchie 1987).

The southeastern range of *Q. macrocarpa* includes Nebraska, Kansas, Oklahoma, western Ohio and western Illinois. This area has an average annual precipitation

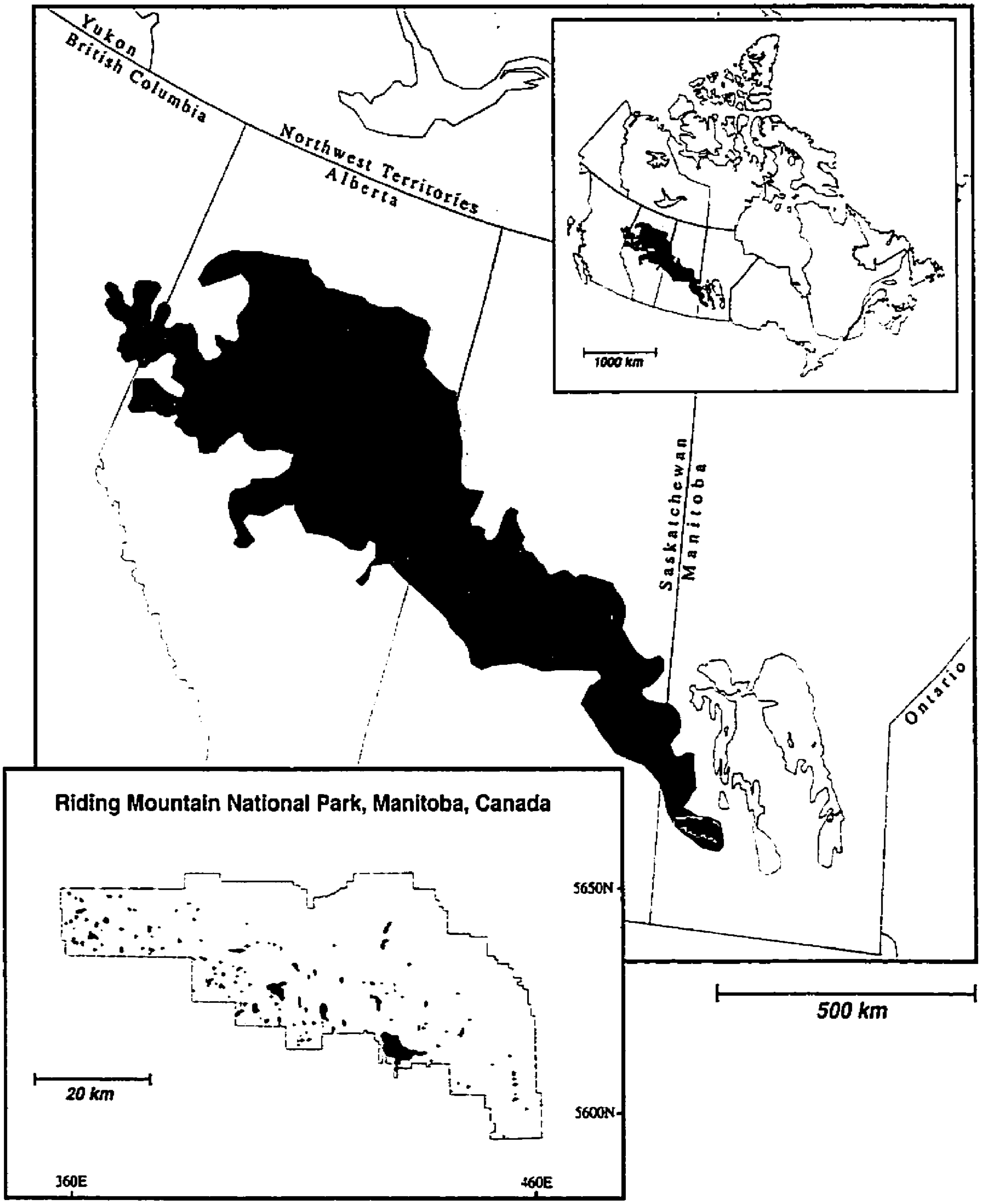


Figure 1.1. Riding Mountain National Park, Manitoba, Canada situated within the Mixedwood Section (B18a; Rowe 1972) of the Boreal Forest Region (shaded area). (figure modified from Johnson 1994).

exceeding 1270 mm, minimum temperatures of -7°C, and a long (250+ days) growing season (Johnson 1990).

The best development of *Q. macrocarpa* occurs in the eastern temperate zone which includes southern Ontario, eastern Wisconsin, Michigan, eastern Indiana, eastern Illinois, New York, New England, and Pennsylvania (Ritchie 1987). This area has an average annual precipitation of approximately 1140 mm which is spread fairly uniformly throughout the year. The summers are hot and humid with the period of mean daily temperature greater than 0°C lasting from April to November. Winters are mild and snowy (Ritchie 1987).

1.1.3 Quaternary Ecology

Glacial History

During most of the Quaternary period, the southern Canadian Interior Plains and northeastern United States were glaciated by the Laurentide Ice Sheet (Ritchie 1985, Delcourt & Delcourt 1989). The ice sheet had retreated to just north of Lake Winnipeg by the beginning of the Holocene (about 10,000 years ago). The resulting meltwater created glacial Lake Agassiz, which covered an area that included most of the central Interior Plains in Canada and the United States (Klassen 1989).

By 9,000 years BP, drainage of Lake Agassiz was almost completed, leaving behind several inland lakes. Just south of Manitoba's lakes, bedrock is deeply buried beneath the silty clays deposited by Lake Agassiz (Delcourt & Delcourt 1989). Throughout most of the region covered by Lake Agassiz are scattered moraines as well as beach ridges. These beach ridges are found at elevations 389 m above sea level west of Morden and 410 m above sea level west of Neepawa.

The dissection of the Manitoba Escarpment by several small creeks also occurred during the Holocene (Delcourt & Delcourt 1989). These creeks, which drain to the Manitoba Lowlands, deeply incise the escarpment of Riding Mountain National Park. Stream incisions of 30 to 60 m are common. At the base of the Escarpment, deposition of eroded shale has produced a series of low-angle alluvial fans.

Climatic conditions similar to those of present were established soon after deglaciation (Klassen 1989). However, varying conditions occurred during deglaciation (Holloway & Bryant 1985). Cold, dry conditions following the retreating glacier created tundra-like ecosystems. The climate was cooler and moister than at present during the early Holocene (about 10,000 years BP). A warming period (Hypsithermal Period) occurred from 6,000 to 4,000 years BP followed by cooler, wetter conditions similar to the present.

Post-Glacial Development of Quercus

Quercus species are notorious for undergoing hybridization, resulting in many intermediate forms which are difficult to distinguish taxonomically (Ritchie 1964). As a result, pollen morphology also intergrades, making it impossible to key out fossil *Quercus* pollen grains. Therefore, the distributional history of *Quercus* is considered at the generic level.

Limited *Quercus* populations persisted in the southernmost boreal forest region during the full-glacial interval 20,000 years ago (Ritchie 1964). This trend of low *Quercus* dominance continued for the next 2,000 years. By 16,000 years BP, *Quercus* populations increased across the southern portion of the distribution of *Quercus*, while in the west, *Quercus* populations declined in Texas. To the north, *Quercus* expanded across the Interior Low Plateaus of Tennessee and into the western Ozarks. By 14,000 years BP, *Quercus* extended nearly to the ice front. The northern range limit continued to extend northward and reached Wisconsin, Minnesota, and southern Manitoba by 12,000 years BP. By 10,000 years BP, the northern limit for *Quercus* reached the northern Great Lakes region near the glacial ice front, and extended from western Minnesota, east of Glacial Lake Agassiz, along the southern shore of Lake Superior, and eastward across central Ontario and southern Quebec to Maine and New Brunswick. The western limit was bounded by the developing prairie-forest ecotone. *Quercus* colonized central and southern Florida with *Quercus* populations reaching 96% dominance. Between 10,000 and 8,000 years BP the western margin of *Quercus* shifted eastward across the central states. The northern range limit extended from northern Minnesota across-central Ontario; southern Quebec, New Brunswick, and Nova Scotia. Population centers of approximately 60% *Quercus* composition were located in the central Atlantic states, southeastern Missouri to central Alabama, and the coastal plain from central Georgia to southern Florida. From 8,000 to 6,000 years BP the climate was warming and the Laurentide Ice Sheet continued to decline. By the end of this period Glacial Lake Agassiz had also drained. However, despite this warming trend the northern and eastern range limit of *Quercus* remained relatively stationary across southern Ontario east to Nova Scotia. Across the Gulf and southern Atlantic Coastal Plains, *Quercus* populations diminished further. However, dominance of *Quercus* was 40% throughout the central portion of its range, with values of over 60% in the central Appalachian Mountains, southern Interior Low Plateaus, Ohio and the Florida Peninsula. By 4,000 years BP, the northern range limit had not changed greatly while the south and east range limits were constrained by the ocean and the prairie to the west. *Quercus* dominance also continued to decrease in the south, gradually being replaced by southern pines on fire-prone upland sites. 2,000 years ago, *Quercus* constituted more than 60% of the forest composition within the central Appalachian Mountains. The northwest limit extended further west into eastern Saskatchewan and by 500 years BP *Quercus* represented less than 20% of the northern hardwoods and southeastern evergreen forest regions.

Quercus followed the retreating glacier closely but seemed to do best in the temperate areas of eastern North America. These areas consistently had higher dominance values of approximately 60%. Lower but constant values of 20% were found near the northern border from eastern Saskatchewan east to Nova Scotia. *Quercus* dominance was probably lower in the north and west due to drier and cooler conditions.

1.1.4 Bedrock and Glacial Deposits

Interior Plains Region

Bedrock geology of the Interior Plains region is mainly of rocks of the Cretaceous age (Klassen 1989). These consist typically of shales, siltstones and sandstones which were laid down in shallow seas. Lower Tertiary deposits are found in the southern and western parts of the Interior Plains and consist mainly of coarse, resistant siltstones and sandstones. Younger Tertiary deposits consisting of coarse to fine sand and quartzite pebble and gravel are found locally in the southern Interior Plains. The nature of the bedrock influenced topographic development, affected the way in which the rock reacted at the base of the glaciers, and played a role in determining the composition of glacial deposits. Glacial deposits in the area are mostly till, with extensive areas of modification due to the drainage of Glacial Lake Agassiz.

Manitoba Region

Today, Manitoba is composed of a variety of geologic landforms, climate, soils, vegetation, and wildlife (Welstead et al. 1996). *Q. macrocarpa* occurs in the southern half of the province on the southwest uplands and the Manitoba lowlands. The surface bedrock south of the Precambrian Shield, which corresponds to the northern range of *Q. macrocarpa*, is new and young. South central and western Manitoba is covered mainly by Paleozoic sedimentary rocks overlaying the Precambrian Shield (Corkery 1996).

The Manitoba Lowlands are the flattest part of the province. The area is developed on Paleozoic limestone and dolomite strata which has been modified by glacial erosion and deposits. Moraines are scattered throughout most of the region as well as beach ridges of former Lake Agassiz. The southwest uplands are characterized by the Manitoba Escarpment. Several valleys which cut into the Escarpment were formed by preglacial rivers. Bedrock is exposed along the escarpment face, but on the plateaus is covered by thick glacial deposits.

Erosional patterns that persist today began to develop on the thick Cretaceous shales that covered most of southern Manitoba 55 million years ago. However, the Manitoba Escarpment is a preglacial feature which was not significantly eroded by glaciation due to the erosion-resistant nature of the overlying hard gray Odanah shale. This shale, which has a high silica content derived from volcanic ash and the remains of siliceous microorganisms, formed a resistant cap to the Manitoba Escarpment and prevented it from being reduced to the same level as the Manitoba Lowlands (Corkery 1996).

Lake Agassiz came into existence about 13,000 years BP as meltwater was contained behind the retreating glacier. The lake rose and fell during glacial advances and retreats, so that at different times it emptied into the Mississippi, the Great Lakes, and the Mackenzie systems. Lakes Winnipeg, Winnipegosis, and Manitoba remain as remnants of the former glacial lake. At its highest point, Lake Agassiz extended far into the Assiniboine embayment, forming strandlines along the Manitoba Escarpment. Beaches of this stage are found today along the east side of Riding Mountain National Park.

Deposition into Lake Agassiz produced the excessively flat land around Winnipeg, north of Portage la Prairie and Dauphin (Corkery 1996). Most of the sedimentation is in the form of alternating thin and thick layers of clay. These layers may represent seasonal deposition with coarse grained layers deposited in summer when no ice occurred on the lake, and fine grained layers deposited in winter when the lake was frozen.

1.1.5 Disturbance History in Riding Mountain National Park

Fire History

Before European settlement, the average length of time between fires may have ranged from five to ten years in prairie areas and from 70 to 100 years in the boreal forest (Riding Mountain National Park 1998). However, conifer forests support large and intense fires during dry, warm periods, while grasslands have low-intensity burns more often.

During the mid-1800's, fires were set in the Riding Mountain region to burn slash and clear land. These fires often escaped into the unsettled highlands, destroying many mature forest stands. These stands were composed primarily of *Picea* species and this is believed to have increased intense fire activity. Between 1885 and 1895, two large forest fires had effectively cleared the remaining forests west of Clear Lake. Most of the *Picea* species were removed, leaving extensive grasslands interspersed with groves of *P. tremuloides* sprouts.

Since then, the decline in the spruce forest, combined with fire prevention and suppression efforts, has decreased the size and intensity of fire in these forest communities. 212 fires have been recorded in the past 55 years in RMNP, but most of them were small and easily extinguished. In all of those fires combined less than 21% of the Park area was burnt.

In the absence of fire, many *Quercus* openings have been invaded by tree and shrub species (Riding Mountain National Park 1998). Over time, these *Quercus* stands may also be replaced by more shade tolerant tree species (Christensen 1977, Lorimer 1984, McCune & Cottam 1985, Nowacki et al. 1990). The lack of fire has also caused the uplands of Riding Mountain National Park to become dominated by *P. tremuloides* forests which are more than 100 years of age (Riding Mountain National Park 1998). However, as the *Picea* component returns and replaces the dominant *P. tremuloides*, the likelihood of large, uncontrollable fires will increase again.

Agriculture/Logging History

By the late 1870's, most of the agricultural land in Manitoba had been surveyed into townships (Riding Mountain National Park 1998). During settlement of the Riding Mountain area, logging occurred in the forested uplands and on the river valley slopes of the Escarpment. Most of the *Q. macrocarpa* on the slopes was harvested during this period, to the extent that no undisturbed stands remain. Logging camps also cut large stands of *Picea*, *Pinus* and *Poplulus*.

In 1895, the Riding Mountain Forest Reserve was established to reduce pressure on the timber resources of the Escarpment, withdrawing the land from settlement. However, controlled harvesting of timber, and grazing and haying continued until 1970. Today, the Park is totally surrounded by agricultural land while natural habitat patches outside the Park are continually being cleared.

1.2 Biology and Ecology of *Q. macrocarpa*

1.2.1 Taxonomic Relationships

The dicot, or Magnoliopsida, class consists of six subclasses (Cronquist 1988). *Quercus* belongs to the subclass Hamamelidae, which is considered to have developed from the Magnoliidae subclass during the Lower Cretaceous, more than a 100 million years ago.

The Hamamelidae subclass is an ancient group of wind-pollinated families with reduced flowers that are often borne in catkins. It originated in a climate with alternating wet and dry seasons and consists of 11 orders, 26 families, and about 3400 species. Approximately one-quarter belong to the order Fagales, which originated approximately 80 million years ago. The Fagales order consists of four families and more than 900 species. The Fagaceae family comprises eight genera, including *Quercus*, *Fagus* (beech), and *Castanea* (chesnut). The *Quercus* genus comprises between 500 and 600 species (Farrar 1995).

1.2.2 North American *Quercus*

Quercus are important tree species in the deciduous forests and savannas of North America, Europe, and Asia. Approximately 60 *Quercus* species occur in the United States and 11 in Canada (Farrar 1995). *Quercus* are classified into two major groups: 'white' and 'red' oak. Species in the white oak group have leaves with large rounded lobes or large, regular teeth and can be easily identified by these features. Tree species in this group include *Q. macrocarpa*, *Q. alba*, *Q. bicolor*, *Q. muehlenbergii*, *Q. prinoides*, and *Q. prinus*. The red oak species have bristle-tipped lobes on the leaves which can vary widely in size and form. Tree species in the red oak group include *Q. rubra*, *Q. velutina*, and *Q. palustris*.

Species in both groups are monoecious (pollen and seed flowers occur separately on the same tree) and wind pollinated. The fruit of both red and white oak species are 1-seeded nuts with a tough leathery shell or acorn, but ripen differently. White oak acorns mature in one growing season and germinate in fall, whereas red oak acorns ripen over two growing seasons and germinate the following spring. Both groups readily produce sprouts on cut or damaged stumps and have deep, wide-spreading root systems with a strong taproot.

Q. macrocarpa occurs in association with the other *Quercus* species listed above in various regions of its range. All species, including *Q. macrocarpa*, form pure stands in localized areas as well as co-occurring with many other tree species. Many of the *Quercus* species reach their northwestern limit in southern Minnesota or northern to central Wisconsin (Rogers 1990, McQuilkin 1990, Sander 1990, Stransky 1990). *Q. macrocarpa* is the only *Quercus* species to surpass these limits, extending its northwest distribution into North Dakota, central Manitoba, and eastern Saskatchewan (Johnson 1990).

1.2.3 Quercus macrocarpa Michx.

Range and Distribution

Q. macrocarpa is the most common species of native 'white' oak in Canada (Johnson 1990). The northwestern limit of *Q. macrocarpa* occurs in the southern edge of the boreal forest and extends south and east into the grassland and the eastern temperate zones (**Fig 1.2**; Ritchie 1987). The northern fringe between the boreal forest, grassland and eastern temperate regions is called a 'tension zone' which occurs near the geographical center of

Canada in Riding Mountain National Park. Many biological elements of the continent are represented in this tension zone, creating a mosaic of plant communities (Riding Mountain National Park 1993). In this area *Q. macrocarpa* occurs in association with many different tree, shrub and herb species. It also occurs as extensive monodominant stands that is most commonly encountered on well-drained, calcareous substrates.

The western limit of *Q. macrocarpa* occurs in a strip of land from eastern Saskatchewan, south to Oklahoma between eastern deciduous forest to the east and prairie to the west (Cottam 1949, Braun 1950, Curtis 1959, Tester 1989, Abrams 1992). Large areas of *Q. macrocarpa* are common in North and South Dakota and comprise almost 20% of the forested land (Johnson 1990). Small islands of *Q. macrocarpa* savanna also occur in Minnesota (Davis et al. 1998, Ritchie et al. 1998), southern Ontario (Szeicz & Macdonald 1991), and Wisconsin (Curtis 1959, Whitford & Whitford 1971, Kline & Cottam 1979).

Within the prairie region, western extensions of deciduous forest grow along streams and rivers forming gallery forests (Wikum & Wali 1974, Killingbeck & Wali 1978). Even though *Q. macrocarpa* is commonly the dominant tree species in these forests, regeneration is often poor (Johnson et al. 1976). Instead, more shade-tolerant, deciduous tree species often dominate the understory (Hosner & Minkler 1963, Laing 1965, Dooley & Collins 1984, Host et al. 1987, Abrams 1992).

To the east of the savanna region, varying densities of *Q. macrocarpa* are found in deciduous forests (Braun 1950, Buell & Cantlon 1951, Carvell & Tryon 1961, Hosner & Minkler 1963, Abrams 1992). Even though *Q. macrocarpa* is common in these forests, it rarely dominates. Instead, it generally occurs as a minor associate in these forest types (Curtis 1959).

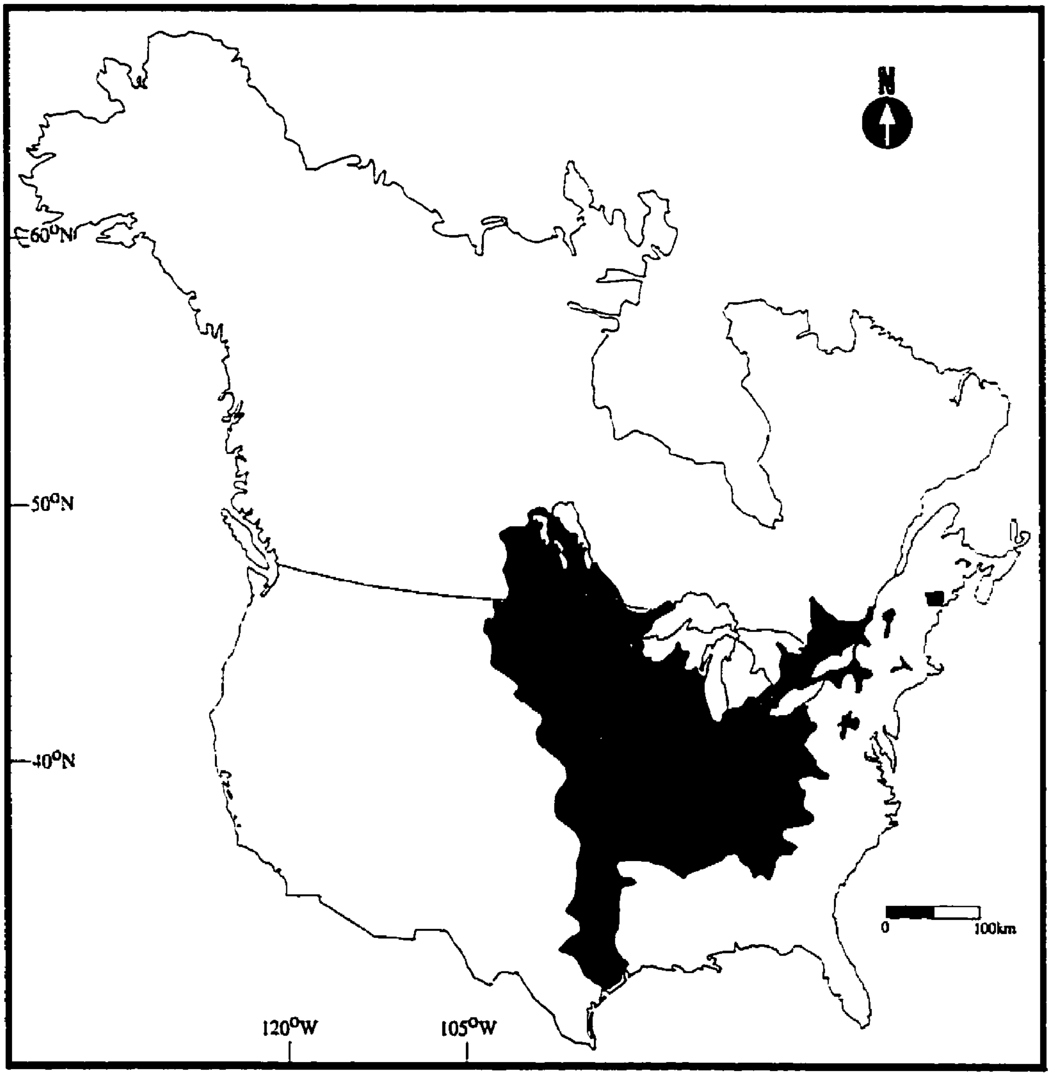


Figure 1.2 Native range of Bur Oak (from Johnson 1990).

Reproduction

Flowering and Fruiting

Male flowers emerge in the spring as drooping, many-flowered, ephemeral catkins. Female flowers emerge as small, reddish, disc-like sessile "blotches" in the leaf axils of the new shoots and appear 5-10 days after the emergence of the male catkins (Farrar 1995). When the female flowers become visible, catkins are 40-60% of their final length, new shoots are about 6 cm in length and new leaves 3-4 cm long. The time of appearance and development of staminate catkins and pistillate flowers varies from year to year depending on weather conditions (Sharp 1967, Ahlgren 1957).

Flower development is considered to be complete when pollen is shed and styles and stigmas have become dry and brittle (Sharp 1967). Pollen from one tree seems to germinate better on stigmas of another, favoring cross-pollination. The fruit, or acorn, then begins a developmental phase. The acorns ripen over the summer and drop from the tree as early as August or as late as November (Johnson 1990).

Seed Production and Dispersal

Q. macrocarpa may bear seed for up to 400 years with a minimum seed bearing age of 35 years and an optimum of 75 to 150 years. Good acorn crops occur every 2 to 3 years with no or light crops in intervening years (Johnson 1990).

Temperature is an important factor influencing the size of the acorn crop in *Q. alba*. A freeze after blooming will kill the emergent flowers. Therefore, acorn production will be reduced or even destroyed for that year (Sharp 1967). Alternatively, good crops of acorns occur when comparatively cool periods follow warm spells early in the flowering season. The warm period increases development of viable pollen, while a cool period later enhances ovary development and fertilization (Sharp 1967, Goodrum 1967, Andersson 1991).

Acorns are dispersed short distances (10 to 30 m) by gravity, water, mice, squirrels and chipmunks (Johnson 1990). Rodents usually hoard acorns very near their source within the animal's home range (Crow 1988). Acorns are often buried, which greatly increases their chance of germinating successfully. Squirrels also disperse acorns away from the parent tree to sites with potentially better growing conditions. Birds such as blue jays can disperse acorns long distances from source trees. Jays have been found to only collect and disperse viable acorns, resulting in the dispersal of seeds of the highest quality and germinability (Darley-Hill & Johnson 1981).

Vegetative Reproduction

Q. macrocarpa may sprout epicormic shoots or 'grubs' (Abrams 1992). These are vegetative growths of the roots that sprout close to the parent tree. Sprouting usually occurs after the parent tree has been cut or burned, but disturbance is not necessary for the parent tree to produce sprouts. Although they grow quickly, the quality of these sprouts is poor (Johnson 1990). In a five year old prescribed burn in Minnesota, 60% of *Q. macrocarpa* with a trunk diameter between 10 and 40 cm had produced sprouts. These sprouts grew in clumps (averaging 21 per tree) with the tallest live stems per clump averaging 2.5 m in height. The number of sprouts produced was found to decrease with increasing age of the tree. Sprouting was also found to increase with increasing scorch height (Sieg & Wright 1996).

Seedling Development

Germination of *Q. macrocarpa* seedlings usually occurs immediately after acorn drop in the fall, but acorns of some northern trees may remain dormant through the winter and germinate the following spring (Johnson 1990). In Iowa uplands, acorn germination was best where litter was removed. When covered by litter, acorns are more liable to pilferage by rodents, and new seedlings are susceptible to fungal and insect attack.

Various factors such as temperature and light intensity affect seedling development. Under a controlled environment. *Q. macrocarpa* seedlings grow fastest at a daytime temperature of 31°C and a nighttime temperature of 19°C. They also produce a greater number of shoots when grown under continuous light (Johnson 1990). Under field conditions, however, *Quercus* seedlings typically produce only one flush of leaves with very little growth occurring during the growing season (Crow 1988).

Both endogenous and exogenous factors determine resprouting in *Quercus* species (Crow 1988). The amount of stored carbohydrate reserves, and a buildup of growth inhibitors affect the growth of *Quercus* seedlings and sprouts. Once the stored carbohydrate reserves are used up, growth depends on translocation from stored carbohydrates or on current production of photosynthate. The shoot elongation period lasts only two or three weeks. Once the shoot becomes dormant the terminal bud forms. The top then dies back during the winter only to resprout the following spring.

Q. macrocarpa is relatively intolerant of flooding (Johnson 1990). First year mortality may be high if seedlings are submerged for more than two weeks during the growing season. Although some *Q. macrocarpa* seedlings can endure flooding for up to 30 consecutive days, root growth is greatly reduced. This in turn reduces drought tolerance after floodwaters have receded.

Root growth of *Q. macrocarpa* seedlings is rapid, and the taproot penetrates deeply into the soil before the leaves unfold (Weaver 1932, Crow 1988). *Q. macrocarpa* seedlings are also efficient users of water. These two characteristics may explain why *Q. macrocarpa* is able to colonize xeric sites and can establish itself successfully in grassland communities (Johnson 1990).

Sapling and Pole Development

Growth Form

Q. macrocarpa is a slow growing tree. Mature trees generally grow to a height of 24 to 30 m on mesic sites (eastern United States and southeast Canada) and live 200 to 300 years. In the prairie border (north central United States and southwestern Manitoba), *Q.*

macrocarpa averaging 9-12 m in height may be found in nearly pure stands. On limestone ridges and steep, south facing slopes the trees may be less than 7 m tall at 150 years of age (Johnson 1990).

Characteristically, *Q. macrocarpa* have a straight trunk with deeply furrowed, fire-resistant bark (Daubenmire 1936). They have a broad, open crown of stout branches which are nearly horizontal in the lower portion of the tree. On xeric sites the trees attain a knarled, stunted growth form with a trunk that divides into radiating, crooked branches (Farrar 1995).

Root Growth

Rapid taproot growth continues in the sapling stage, with abundant lateral growth as well (Johnson 1990). The taproot has been found to develop 30 or more large main branches in the first 2 feet of soil. At this stage, root biomass equals that of the aboveground portion (Weaver 1932).

Root growth continues for most of the year, allowing the tree to exploit new water reserves (Dougherty 1981). Factors such as soil texture and composition, the availability of nutrients and water, and root competition affect root development. *Q. macrocarpa* trees are very adaptable, and readily form a deeper root system during periods of water-stress (Weaver 1932).

Genetics

A northern variety of *Q. macrocarpa*, *Q. macrocarpa* var. *olivaeformis*, has been recognized. It has an acorn size about half that of the southern form, and the acorn cup is much thinner and smaller. These acorns germinate in spring following seedfall rather than soon after falling in the autumn. In eastern Nebraska where the two forms are found in the same locality, the southern form of *Q. macrocarpa* is more common in moister sites (Johnson 1990).

Q. macrocarpa hybridizes with nine other *Quercus* species, however the cross with *Q. alba* is the most frequent hybrid, and is widespread within the overlapping ranges of the two species.

Associated Species

Q. macrocarpa tolerates a wide range of soil and moisture conditions, allowing it to grow in association with a number of tree species in oak savanna, gallery, and closed deciduous forests (Johnson 1990).

Q. macrocarpa is one of the major tree species present in the oak savannas of the prairie-forest transition zone in Wisconsin, Minnesota, Iowa, and Illinois. Shrubs are especially abundant in *Q. macrocarpa* stands of the Great Plains region. Predominant among them are *Corylus cornuta*, *Corylus americana*, *Symphoricarpos orbiculatus* and *Rhus glabra*. Common associates on the prairie borders are *Crataegus chrysocarpa*, *Symphoricarpos occidentalis* and *Malus ioensis* (Curtis 1959, Johnson 1990, Abrams 1992).

Q. macrocarpa is also an associate of many other tree species in the northwestern part of its range (southern Manitoba and eastern Saskatchewan). Here it grows in mixed stands of *U. americana*, *F. pennsylvanica*, *P. tremuloides*, *A. negundo*, and *Picea glauca* on mesic sites. It also occurs in pure stands in xeric, gravelly sites (Bird 1961, Wikum & Wali 1974, Keammerer et al. 1975, Johnson et al. 1978, Killingbeck & Bares 1978, Reily & Johnson 1982).

In the southern gallery forests of Kansas and Oklahoma important associates of *Q. macrocarpa* are *Q. palustrus*, *Liquidambar stryaciflua*, *A. rubrum*, *U. americana*, *Nyssa sylvatica*, *Q. bicolor*, *Q. phellos*, *Q. lyrata*, *F. pennsylvanica*, *Q. nuttallii*, *Q. michauxii*, *Carya laciniosa*, and *Carya ovata*. Shrubs and vines in these sites include *Ilex decidua*, *Rhus radicans* and *Campsis radicans* (Dooley & Collins 1984, Abrams 1986, Johnson 1990).

In the deciduous forests of southeastern Ontario and the northeastern United States, important associates of *Q. macrocarpa* include *F. nigra*, *U. americana*, *A. rubrum*, *Tilia americana*, *A. saccharum*, *Plantanus occidentalis*, *Tsuga canadensis*, and *P. deltoides*. Common shrub associates include *Alnus rugosa*, *Cornus stolonifera*, and *Toxicodendron vernix* (Braun 1950, Curtis 1959, Johnson 1990, Abrams 1992).

In the deciduous forests of the southeastern United States, important associates of *Q. macrocarpa* include *Q. rubra*, *Q. velutina*, *Q. montana*, *Q. coccinea*, *C. tomentosa*, *C. glabra*, and *C. cordiformis*. In this forest type, associated shrubs and vines include *Hamamelis virginiana*, *Vitis* species, *Parthenocissus quinquefolia*, and *R. radicans* (Braun 1950, Carvell & Tryon 1961, Hosner & Minckler 1963, Johnson 1990).

1.3 Trees Associated With *Q. macrocarpa* In Manitoba

1.3.1 Fraxinus pennsylvanica Marsh.

Distribution

F. pennsylvanica is the most widely distributed of all the American ashes. It is adaptable to harsh conditions, but shows best growth in moist bottomlands and stream banks. The species occurs from Cape Breton and Nova Scotia west to southeastern Alberta, south through central Montana, northeastern Wyoming, to southeastern Texas, and east to northwestern Florida and Georgia (Kennedy 1990). Climate is subhumid to humid, with annual precipitation varying from 380 to 1520 mm with warm season precipitation of 250 to 890 mm. Temperatures range from -18° to 13° C in January to 18° to 27° C in July. The average length of frost-free season is 120 to 280 days.

F. pennsylvanica is probably the most adaptable of all the ashes. It grows naturally on a range of sites from clay soils subject to flooding, to sandy or silty soils where available moisture is limited. However, it grows best on fertile, moist, well-drained soils. *F.*

pennsylvanica is most commonly found on alluvial soils along rivers and streams and less frequently in swamps.

Reproduction

F. pennsylvanica is dioecious. The small, usually inconspicuous flowers appear in the spring, at the same time or just before the leaves appear. Usually, flowering starts when trees are 8 to 10 cm in diameter and 6 to 8 m tall. Flowers appear as early as March or April in Florida, and from late April to early May in the northern part of its range. The pollen is disseminated by wind and is dispersed over relatively short distances.

Ash fruits are elongated, winged, single-seeded samaras borne in clusters. Unpollinated flowers or flowers pollinated by an incompatible ash species drop off within the first month. *F. pennsylvanica* seeds start to fall as soon as they ripen and continue to fall into the winter. Most seeds are dispersed by wind within short distances of the parent. Stumps of sapling and pole-size *F. pennsylvanica* sprout readily.

Growth Form and Reaction to Competition

F. pennsylvanica grows a tall, straight bole in mesic conditions for half the height of the tree, after which it forks or crooks. *F. pennsylvanica* seedlings have been found to withstand flooding conditions for up to several months.

F. pennsylvanica varies from intolerant to moderately shade tolerant in the northern part of its range. It colonizes early in succession on alluvial soils, either as a pioneer species or following *P.deltoides* or *P. tremuloides*. It is less able to maintain its position in the crown canopy than some of its more rapidly growing associates, such as *A. rubrum* and *U. americana*.

Associated Species

Species most commonly associated with *F. pennsylvanica* are *A. negundo*, *A. rubrum*, *Celtis laevigata*, *Platanus occidentalis*, *P. tremuloides*, *U. americana* and other *Quercus* species.

1.3.2 Acer negundo L.

Distribution

A. negundo is one of the most widespread and best known of the maples. Its greatest value may be in shelterbelt and street plantings in the Great Plains, where it is used due to its drought and cold tolerance (Overton 1990).

In Canada, the species occurs in the Great Plains from eastern Alberta to central Saskatchewan and Manitoba, and in southern Ontario. In the United States it is found from New York to central Florida and west to southern Texas. Isolated western populations also occur. In California, *A. negundo* grows along river valleys and on the western slopes of the San Bernardino Mountains. The species occurs as far south as Guatemala. This range demonstrates that species is well adapted to variety of climatic conditions.

Although *A. negundo* is most commonly found on moist soil, it is drought tolerant. It commonly occurs on deep alluvial soils near streams, but also appears on upland sites and occasionally on poor, dry sites. *A. negundo* has been found on virtually all types of soils, from heavy clays to pure sands.

Reproduction

A. negundo is dioecious with imperfect flowers. Flowers appear during or before the leaves from March to May, depending on geographic location. Seed crops are produced each year beginning at age 8 to 11. Ripening takes place from August to October, and seeds are wind-distributed. Vegetative reproduction from young, vigorous trees and fallen trunks is common.

Growth Form and Reaction to Competition

A. negundo is a small to medium-size tree reaching 15 to 23 m in height and 60 to 120 cm in diameter. It typically forms a short, tapering bole and a bushy, spreading crown. *A. negundo* is a short-lived species, attaining an average age of 60 years but rarely 100 years. Growth during the first 15 to 20 years is very rapid, adding up to 2.5 cm per year in diameter. The species typically develops a shallow, fibrous root system (Overton 1990).

A. negundo is a shade tolerant species which follows species such as *P. deltoides* and willow in colonizing new ground. In some instances it is a pioneer species in the invasion of old fields. In the central portion of its range, it may persist for some time in *Quercus-Carya* forest but is eventually eliminated due to shading.

Associated Species

Associated eastern species include *A. rubrum*, *T. americana*, *N. sylvatica*, and *Q. lyrata*. In the Plains region, *A. negundo* may occur with *F. pennsylvanica*, *Q. macrocarpa*, *U. americana*, and *Salix* species. In the Rocky Mountains and the Colorado Plateau, associates include several *Salix* and *Populus* species.

1.3.3. Populus tremuloides Michx.

Distribution

P. tremuloides is the most widely distributed tree in North America. It grows on many soil types, especially sandy and gravelly slopes, and is quick to pioneer disturbed sites where there is bare soil. This fast-growing tree is short lived, and pure stands are gradually replaced by slower-growing species (Perala 1990).

The range of *P. tremuloides* extends from Newfoundland and Labrador west across Canada along the northern treeline to northwestern Alaska, and southeast through Yukon and British Columbia. Throughout the western United States, it is most commonly found in the mountains from Washington to California, southern Arizona, throughout Texas, and northern Nebraska. From Iowa and eastern Missouri it ranges east to West Virginia, Pennsylvania, and New Jersey. *P. tremuloides* is also found in the mountains of Mexico.

Climatic conditions vary greatly over the range of the species, especially winter minimum temperatures and annual precipitation. The widest range of temperatures endured by aspen occurs is in Montana, where January lows of -57° C and summer highs of 41° C have been recorded. In Alaska and northwest Canada, part of the range lies within the permafrost zone, but *P. tremuloides* grows only on the warmest sites that are free of permafrost.

P. tremuloides grows on a great variety of soils, ranging from shallow and rocky to deep loamy sands and heavy clays. It is most abundant and grows best on warm south and southwest aspects in Alaska and western Canada. It is common on all aspects in the western mountains of the United States and grows well wherever soil moisture is not limiting. In the Prairie Provinces of Canada, particularly near the border between prairie and woodland, the species may be confined to cooler and moister north and east facing slopes and to small depressions (Bird 1961).

Reproduction

P. tremuloides is primarily dioecious. The pendulous flower catkins, 3.8 to 6.4 cm long, generally appear in April or May (mid-March to April in New England, May to June in central Rockies) before the leaves expand. Flowers are pollinated by wind (Perala 1990).

Good seed crops are produced every 4 or 5 years, with light crops in most intervening years. Some open-grown clones may produce seeds annually, beginning at age 2 or 3. The minimum age for large seed crops is 10 to 20; the optimum is 50 to 70. Seeds begin to be dispersed within a few days after they ripen and seed dispersal may last from 3 to 5 weeks. The seeds, buoyed by the long silky hairs, can be carried for many kilometers by air currents. Water is also a dispersal agent. Vegetative sprouting from surface roots is common, but mature trees may lose this ability.

Growth Form and Reaction to Competition

P. tremuloides is a small to medium-sized, fast-growing, and short-lived tree. Under the best of conditions it may attain 36.5 m in height and 137 cm diameter. Although individual ramets of a clone may be short-lived, the clone itself may be thousands of years old (Perala 1990).

Height growth of the young trees is rapid for about the first 20 years and slows thereafter. High mortality through self-thinning characterizes young *P. tremuloides* stands regardless of origin. In both seedling and sucker stands natural thinning is rapid, and ramets that fall below the canopy stop growing and die within a few years.

In both the eastern and western parts of its range, *P. tremuloides* is classed as very shade-intolerant, a characteristic it retains throughout its life. *P. tremuloides* is an aggressive pioneer species, and quickly suckers back following logging or fire.

Associated Species

P. tremuloides grows with a large number of trees and shrubs over its extensive range. In southern Manitoba, it is most commonly associated with *Q. macrocarpa* (Bird 1961).

1.4 *Quercus macrocarpa* Communities In North America

Q. macrocarpa occurs in the eastern deciduous forests of North America, and extends into the grasslands of the Great Plains along river systems as gallery forest (Severson & Kranz 1978, Abrams 1986, 1992). It also forms savannas and woodlands along the prairie-forest ecotone (Curtis 1959). These communities are difficult to separate out, however, as they form a continuum from prairie through savanna and woodland to closed-canopy forest (Leach & Ross 1995).

1.4.1 Oak Savanna/Woodland

Savanna is defined as a sparsely treed grassy plain in tropical and sub-tropical regions (Concise Oxford Dictionary 1995). However, the term is often applied to sparsely forested grasslands in the central United States and Canada (Buell & Cantlon, 1951, Rice 1959, Bray 1960, Laing 1966, Whitford & Whitford 1971, Kline & Cottam 1979, Dooley & Collins 1984, Tester 1989, Mlot 1990, Szeicz & Macdonald 1991, Abrams 1992, McClain 1993, Ritchie 1998). In this context, savanna refers to a grassy plain in any climate with few to several open-grown trees resulting in considerable light penetration to the understory (Leach & Ross 1995). Woodland refers to sites that are more open than forests but less open than savannas. Unlike savannas, the understory is not the dominant layer in woodlands (Faber-Langendoen 1995). Woodlands have 25-80% tree cover, whereas savannas have 5-30% tree cover.

Oak savannas and woodlands are often referred to as "oak barrens", "oak openings", "wooded grassland" and "shrub grassland" (Whitford & Whitford 1971, Faber-Langendoen 1995). The term woodland has not been widely used in North America (Faber-Langendoen 1995). Since the term savanna and woodland have not been defined until recently and are used interchangeable in the literature, oak savanna will refer to both communities in this review.

Oak savanna occurs on xeric sites throughout the range of *Q. macrocarpa* (Wikum & Wali 1974, Johnson 1990). *Q. macrocarpa* is well adapted to these sites due to its tolerance to periodic drought and high light (Abrams & Knapp 1986, Hamerlynck et al. 1994). *Q. macrocarpa* seedlings are well adapted to colonizing savanna grasslands.

Historical Development of Oak Savanna

Oak savanna occurs between the tallgrass prairie to the west and the deciduous forest to the east (Cottam 1949, Curtis 1959, Tester 1989, Abrams 1992). It normally occurs at the western edge of the distribution of *Q. macrocarpa*. Prior to European settlement, it covered 11-13 million ha of the midwest (McClain et al. 1993).

The distribution of grasslands, savannas, and forests reflects general climate patterns, with precipitation decreasing and drought frequency increasing from east to west (Curtis 1959, Leach & Ross 1995). This east-west climatic gradient also affects fire regimes. Infrequent fires in the east both terminate and initiate long-lived species. Moving westward, increasing fire frequency prevents excessive fuel buildup and limits the invasion of fire-intolerant species (Leach & Ross 1995). This results in an east to west gradient of decreasing tree species density and diversity. The thick bark, drought tolerance, and sprouting capability of *Quercus* species promoted their persistence in fire-prone savanna habitats (Hengst & Dawson 1994).

Fire sources in the central Great Plains of North America include lightning strikes, and various activities of aboriginal people such as cooking and the deliberate setting of fires to drive game (Day 1953). Following European settlement, fire frequency declined as agriculture, cattle grazing, road construction, the expansion of towns and active wildfire suppression increased (Abrams 1986). During this period, forests composed mainly of *Quercus* species rapidly expanded into the prairies. *Q. marilandica* and *Q. stellata* forests colonized grasslands in central Oklahoma (Howell & Kucera 1956). *Q. alba*, *Q. macrocarpa* and *U. americana* were the major colonizers in central Missouri (Rice & Penfound 1959), while *Q. macrocarpa* and *Q. muehlenbbergii* were important in eastern Kansas (Abrams 1986). Following European settlement of Wisconsin, fire suppression resulted in the conversion of *Q. macrocarpa* savannas to closed forests of *Q. alba*, *Q. velutina* and/or *Carya* sp. (Cottam 1949, Dorney & Dorney 1989).

Oak Savanna in North America

Oak savannas in the Midwest of North America fall into two categories: those occurring on dry sites, and those of more mesic sites (Haney & Apfelbaum 1993). Dry sites are characterized by *Q. velutina*, *Q. stellata*, *Q. marilandica*, *Carex pensylvanica*, and *Corylus* species. Mesic savannas, which include *Q. macrocarpa*, *Q. alba*, *Q. rubra*, and *Q. bicolor*, are especially vulnerable to rapid invasion by shade tolerant species in the absence of fire. Invading tree and shrubs species include *A. rubrum*, *Prunus serotinia*, *T. americana*, *A. negundo*, and *F. pennsylvanica*. Mesic savannas are therefore more easily degraded and require more effort to restore than dry site savannas.

Northwest Region

In the Black Hills of South Dakota, *Q. macrocarpa* occurs as an short-statured understory species in *Pinus ponderosa* stands on sandstone and shale outcrops (Severson & Kranz 1978, Uresk & Painter 1985, Sieg & Wright 1996). Stunted *Q. macrocarpa* trees also occur on xeric slopes and flats in southwestern Manitoba (Riding Mountain National Park 1993). Monodominant stands of *Q. macrocarpa* are found throughout North Dakota and southern Manitoba (Bird 1961, Johnson 1990, Riding Mountain National Park 1993). Other trees found in varying amounts in these stands include *P. glauca*, *Betula papyrifera*, and *P. tremuloides* (Bird 1961, Uresk & Painter 1985). Understory species present may include *Berberis repens*, *Prunus virginiana*, *Amelanchier alnifolia*, *Symphoricarpos albus*, *Oryzopsis asperifolia*, *Danthonia intermedia* and *Poa pratensis*.

Q. macrocarpa also occurs to adjacent mixed-grass prairie in western South Dakota, often in mixture with *P. tremuloides*. Forbs present in these areas include *Andropogon scoparius*, *Andropogon gerardi*, *Agropyron smithii*, and *Stipa viridula* (Sieg & Wright 1996).

Central Plains Region

Open stands of *Q. macrocarpa* occur on the midslopes of deeply dissected till and bedrock uplands in southeastern Nebraska, while the bottomlands are occupied by gallery forest (Laing 1966). In northeastern Kansas savanna, *Q. macrocarpa* and *Q. prinoides* are co-dominants on upland, xeric terraces of gallery forests (Hamerlynck & Knapp 1994). Both *Q. macrocarpa* and *Q. prinoides* are well-adapted to drought and full sunlight, facilitating their establishment within grasslands (Abrams 1992). *Q. prinoides* is considered to be even more drought-tolerant than *Q. macrocarpa*, and it is more commonly encountered on upland, xeric sites (Hamerlynck & Knapp 1994). *Q. macrocarpa* is more successful on mesic sites with deep soils. It is also better acclimated than *Q. prinoides* to low light levels, allowing it to persist under a more closed canopy.

Northeast Region

Mixed *Q. macrocarpa-Q. rubra* savanna occurs in small areas of east-central Minnesota (Davis et al. 1998, Ritchie et al. 1998). Soils in this region are generally well-drained, well-sorted fine and medium sands which are low in organic matter and poor in nitrogen. Common understory species include *C. cornuta*, *Rosa arkansana*, *A. gerardi*, *Sorghastrum nutans*, *P. pratensis*, *Stipa spartea*, *Asclepias tuberosa*, *Asclepias syriaca*, *Ambrosia coronopifolia*, *Lithospermum carolinense*, *Comandra richardsoniana*, *Artemisia ludoviciana*, *Lathyrus venosus*, *Amorpha canescens*, and *Lespedeza capitata*.

Small pockets of oak savanna occur in southern Ontario north of Lake Erie. These are surrounded by eastern deciduous forest to the east and *Pinus strobus* savanna to the west (Szeicz & Macdonald 1991). *Q. velutina* and *Q. alba* are the dominant tree species with *Q. macrocarpa*, *Q. palustris* and *Q. rubra* as subdominant tree species. The understory is dominated by sedges and grasses such as *Andropogon* and *Poa* species.

In Ontario, presettlement oak savanna was reported to occur from south of Windsor, on the south and east shores of Lake St. Clair, along the lower Thames River in Kent County, west of London, north of Turkey Point on Lake Erie, and around Brantford. It is unlikely that Native people maintained the oak savanna by burning repeatedly as they were nomadic and did not settle permanently in an area (Szeicz & Macdonald 1991). An alternative hypothesis to explain the development of oak savanna in southern Ontario is climate change. A period of warm and dry conditions occurred between 8,000 and 4,000 BP. The change from eastern *P. strobus* savanna to oak savanna in the west and hardwoods to the east may have reflected decreasing summer temperatures, increasing winter temperature and increasing precipitation. Only a small number of oak savanna stands remain in the region, and these occur exclusively on coarse soils developed on outwash sands and gravel.

Oak savanna in Wisconsin is scattered throughout the state (Curtis 1959, Whitford & Whitford 1971, Kline & Cottam 1979). Frequently encountered species in the understory of these stands include *Amphicarpa bractetata*, *Euphorbia corollata*, *Galium boreale*, *Monarda fistulosa*, *Rosa* species, *C. racemosa*, *C. americana*, and *Apocynum androsaemifolium*.

In presettlement times, oak savanna constituted the most widespread plant community in Wisconsin (Curtis 1959). However, much of the savanna forest was cleared for agriculture following European settlement. While some of the remaining oak savanna has retained its original structure and tree cover due to grazing, most stands have succeeded toward a more closed mixed forest of *P. serotinia*, *A. negundo*, and *U. americana* as a result of fire suppression.

In the central United States, the remaining savannas are most commonly composed of *Q. macrocarpa*, *Q. velutina*, and *Q. alba* (McCune & Cottam 1985), with *Q. velutina* most commonly found on sandy soils (Whitford & Whitford 1971). Some mixed *Q. alba-Q. velutina-Q. macrocarpa* savannas in southern Wisconsin have shifted dominance from fast growing *Q. velutina* to slower growing *Q. alba*, with *Q. macrocarpa* as a minor associate (McCune & Cottam 1985). However, the latter two species are shade intolerant as shown by their current failure to regenerate. Also, oak wilt disease has reduced the *Q. velutina* population.

1.4.2 Gallery Forests

Gallery forests are extreme western extensions of the eastern deciduous forests of North America (Wikum & Wali 1974, Killingbeck & Wali 1978). The term 'gallery forest' refers to narrow bands of forest that occur along streams and rivers in the Great Plains (Weaver 1960, Severson & Kranz 1978, Dooley & Collins 1984, Abrams 1986, 1992). They extend into the oak savanna and prairie, creating a mosaic of prairie and forest communities on the landscape (Weaver 1954).

Gallery forests occupy the bottom ravine slopes or lower terraces adjacent to watercourses west of the normal distribution of deciduous species (Abrams 1986). Generally, these deciduous species are unable to grow in the drier environments of the prairie and savanna regions. Increased soil moisture and clay soils adjacent to the rivers allows these tree species to persist in areas well outside their normal ranges (Weaver 1954).

Historical Development

Gallery forests expanded following European settlement of savanna and prairie riverine ecosystems (Bragg & Hulbert 1976). Active fire suppression resulted in the expansion of woody vegetation throughout much of the Great Plains (Sauer 1950, Buell & Cantlon 1951). Prior to European settlement, the limited extent of these forests was probably attributable to higher fire intensity and frequency caused by aboriginal activity (Abrams 1992). The grasslands of Kansas were first invaded by various shrub species, *Q. muehlenbergii*, and *Q. macrocarpa* (Abrams 1986). *Q. velutina*, *Q. rubra*, and *C. ovata* replaced the *Q. prinoides* and *Q. macrocarpa*, and these were subsequently displaced by mesophytic forests dominated by *T. americana* and *Ostrya virginiana*. Currently, it appears that succession from shade intolerant *Quercus* species to more shade tolerant hardwoods is still occurring (Abrams 1992).

Gallery Forests in North America

Northwest Region

Much of the gallery forests of North Dakota and Manitoba occur along the Missouri and Red River Valleys, and are surrounded by agricultural land and native mixedgrass prairie (Keammerer et al. 1975). Common shrub associates in these gallery forests include *C. cornuta*, *C. stolonifera*, *S. occidentalis*, *R. radicans*, *P. virginiana*, *A. alnifolia*, *Parthenocissus inserta*, and *Vitis vulpina*.

Dams have permanently flooded much of the bottomland forests of the upper Missouri River (Keammerer et al. 1975). Lake Sakakawea, which was created by the Garrison Dam, has flooded the bottomland forests of North Dakota from Riverdale to within a few miles of the Montana-North Dakota border. Without the threat of flooding, more land is being cleared for agricultural use. Gallery forests have also been affected by other disturbances such as logging, insects, disease, drought, herbicide spraying and cattle grazing. Thus, the once extensive forests of the floodplain have been greatly reduced.

Both the Missouri and Red River Valleys consist of a series of terraces, but *Q. macrocarpa* only occurs on the uppermost terrace (Wikum & Wali 1974, Keammerer et al. 1975). Upper terrace soils consist of recent alluvial deposits, and are mostly medium-textured and calcareous loam soils. *Q. macrocarpa* does not occur in the dense closed forests of the lower terraces, in part because its seedlings are relatively shade-intolerant. *Q. macrocarpa* generally occurs in the most mature stages of floodplain forest development, and is confined to sites adjacent to prairie bedrock terraces that are well removed from recurrent and prolonged flooding (Johnson et al. 1976, Reily & Johnson 1982).

Q. macrocarpa was found to grow in association with *F. pennsylvanica*, *A. negundo* and *U. americana* in upland, mesic sites (Wikum & Wali 1974, Johnson et al. 1976, Reily & Johnson 1982). Mixed *F. pennsylvanica-Q. macrocarpa* stands are restricted to soils with higher nutrient levels (Killingbeck & Bares 1978). *F. pennsylvanica* trees are generally younger and usually occur under an open *Q. macrocarpa* canopy (Wikum & Wali 1974).

Mixed stands of *U. americana*, *A. negundo* and *Q. macrocarpa* occur exclusively on south-facing, moderately sloped riverbanks. *Q. macrocarpa* regeneration in these galley forests is generally low (Johnson et al. 1976). For this reason, it has been speculated that *F. pennsylvanica* will eventually dominate these sites, with *U. americana* and *A. negundo* as stable secondary associates.

Q. macrocarpa reaches its western limit in the Black Hills of western South Dakota and the Bear Lodge Mountains of northeastern Wyoming (Severson & Kranz 1978). In these areas, *Q. macrocarpa* occurs as large trees in gallery forests at lower elevations between *P. ponderosa* stands and the grasslands.

Central Plains Region

Groves of *Q. macrocarpa* occur in closed canopy gallery forests in the Salt Creek watershed in southeastern Nebraska (Laing 1965). The wide floodplains were covered with tall grass prairie prior to settlement, but most of this former prairie is now under cultivation. Present forest undergrowth in the oak stands is similar to that of the past, with a nearly continuous herb layer of *Laportea canadensis*. *Quercus* seedlings in these sites are therefore doubly shaded, making regeneration unlikely. Replacement of these *Q. macrocarpa* forests by other hardwood species is therefore hypothesized.

Gallery forests in northeast Kansas have dramatically increased since European settlement (Abrams 1986). Currently *Q. macrocarpa* and/or *Q. muehlenbergii* dominate these forests (Abrams 1984, Knapp 1992, Hamerlynck & Knapp 1994), with either species representing the largest and oldest species in each stand surveyed (Abrams 1986). However, numerous *Celtis occidentalis* and *U. americana* saplings (< 50 years old) are present in these stands, suggesting their increased dominance in the canopy over time. Even though *U. americana* is a dominant reproducer, it may not attain dominance in the overstory due to Dutch Elm Disease. *C. occidentalis* may be the climax species on the mesic floodplain forests (where it is already the dominant species), even though it is smaller and not as long-lived as *Q. macrocarpa*. On the steeper, drier sites young *Q. muehlenbergii* and *C. occidentalis* are rare and young *Cercis canadensis* and *U. americana* dominate the understory. Again, since the future of *U. americana* is uncertain, *C. canadensis* seems the most likely species to replace *Q. muehlenbergii*. A successional sequence involving *Quercus* replacement by *C. occidentalis* in mesic sites and by *C. canadensis* in xeric sites therefore seems likely.

In southwestern Oklahoma, gallery forests have developed from Oak savanna near streambeds and rivers on loamy, well-drained soils (Dooley & Collins 1984). The dominant tree species in these forests include *Q. stellata*, *Q. marilandica* and *Juniperus virginiana*. Even though *Q. stellata* dominates these forests, the seedling layer is most often dominated by *C. occidentalis*, *U. americana*, *C. illinoensis*, and *Q. macrocarpa*. *Diospyros virginiana*, *Q. stellata* and *Q. shumardii* were until recently not commonly encountered in southwestern Oklahoma, indicating migration of deciduous forest trees onto the adjacent Oak savanna.

Bottomland gallery forests in southern Illinois generally occur on flat terrain, particularly on terraces formed by older drainage systems not subject to flooding (Hosner & Minckler 1963). Variations in elevation are associated with differences in soils, drainage conditions and tree species. *Q. macrocarpa* is found in older forest stands on the better drained upper terraces. On these sites, the expected climax community is a mixture of the hardwoods *F. pennsylvanica*, *A. negundo*, *U. americana*. *A. rubrum*, *P. deltoides*, and *C. occidentalis* tend to outcompete *Q. macrocarpa* seedlings in regenerating forests. *Q. macrocarpa* may also occur in association with *Q. palustris*, *A. rubrum*, *Gleditsia triancanthos*, *Q. bicolor*, and *Q. lyrata* in the poorly drained areas on lower terraces when surface drainage conditions improve. All species are expected to reproduce and survive in these sites.

1.4.3 Eastern Deciduous Forests

The deciduous forests of eastern North America are a complex vegetational unit composed of both broad-leaved and needle-leaves species (Braun 1950). The development of these forests is due, in large part, to climate patterns. In the west where annual precipitation is lower, deciduous forests occupy more confined sites in ravines and valleys while prairie dominates the uplands. Northward, deciduous species are confined to more favorable sites due to the shorter growing season and extreme winter temperatures. Mixed stands of conifers and broad-leaved trees are characteristic of more northern forests. Deciduous forest stands extend eastward to the Atlantic coast, but as one moves south pines become increasingly important.

Eastern deciduous forests consist of several climax association that include a number of genera, including *Quercus, Acer, Fagus, Tilia, Carya, Fraxinus, Ulmus, Betula, Liriodendron*, and *Castanea* (Braun 1950). These forests have been termed *Quercus-Fagus* formations, since these two genera are represented in most stands (Weaver & Clements 1938). In the eastern deciduous forests of North America, *Quercus* species are one of the most dominant groups (Abrams 1992). Although many *Quercus* species occur throughout the deciduous forests of eastern North America, only areas that include *Q. macrocarpa* are discussed here.

Historical Development

Prior to European settlement, northern hardwood forests extended from northern Minnesota to New England (Abrams 1992). These forests generally contained only a small *Quercus* species component, and were dominated by *Tsuga canadensis, A. saccharum, Fagus grandifolia*, and various species of *Pinus* (Whitney 1986). Fires were infrequent in most of these forests (Lorimer 1977), but drier upland stands burned more frequently and had higher abundance of *Quercus* species (Abrams 1992). Following European settlement, *Q. rubra* colonized a variety of sites, including cut or burned stands on sandy soils as well as sites that had previously been dominated by *P. resinosa* and *P. strobus* (Crow 1988). *Q. rubra* was favored by the logging of *P. strobus*, as this resulted in release of the advance regeneration layer and dispersal of *Quercus* seeds. Other *Quercus* species (including *Q. macrocarpa*) also occupy these sites, but only as a minor associate.

Eastern Deciduous Forests of North America

<u>Fagus-Acer Forest Region</u>

The *Fagus-Acer* forest is entirely contained within an area once covered by the Wisconsin ice sheet (Braun 1950). This forest region extends from central Michigan eastward into southern Ontario and south to the till plains of northern Ohio and western Pennsylvania. The predominant *Quercus* species in the *Fagus-Acer* forest is *Q. alba*; *Q. macrocarpa* is only a minor associate.

In the southwestern part of the *Fagus-Acer* region in Indiana, the current forest is thought to be a seral stage in a successional sequence leading to the establishment of mixed mesophytic stands (Braun 1950). *F. grandifolia* and *A. saccharum* are not regenerating in the understory, but *T. americana* and *Aesculus glabra* are regenerating. This suggests a successional trend toward an *Acer-Tilia* forest.

In eastern Minnesota, the pollen record indicates that forests in the area once contained *Fagus* species. These former *Fagus-Acer* forests have developed into *Acer-Tilia* stands (Buell & Cantlon 1951, Braun 1959). *A. saccharum* seedlings are abundant, while regeneration of *Tilia* is primarily from stump sprouts. Other tree species found in these forests include *P. strobus*, *Abies balsamea*, *P. glauca*, *Betula papyrifera*, *F. pennsylvanica*, *Q. macrocarpa* var. *olivaeformis*, *U. americana*, and *P. tremuloides*. *P. strobus* is represented by a few large individuals that tower over broadleaf canopy. *Q. macrocarpa* in these stands are large, but the species is poorly represented in the regeneration layers.

Quercus-Carya Forest Region

The eastern section of the *Quercus-Carya* forest type extends eastward from the Mississippi River across Illinois and western Indiana, with outliers in central Ohio and southern Wisconsin. The *Quercus-Carya* forest region is considered a tension zone between the *Fagus-Acer* communities and the mixed mesophytic forest communities. Common tree species include *Q. alba*, *Q. velutina*, *Q. rubra*, *Q. macrocarpa*, *C. ovata*, *C. cordiformis*, *F. pennsylvanica*, *U. americana*, *T. americana*, *J. nigra*, *P. serotinia*, *Ostrya virginiana* and *A. saccharum*. On upland sites, *Q. alba* and *Q. velutina* are usually the dominant species. In more mesic conditions, *Q. rubra* and *A. saccharum* commonly accompany the dominant *Q. alba*.

Throughout this forest region, a mixed forest community commonly occupies ravine slopes. *A. saccharum* dominates in the central region and *Carya* species in the east, while *Q. rubra* and *T. americana* are codominant with *A. saccharum* in the west (Braun 1950). The major *Quercus* species on fertile lower and middle-third slopes in West Virginia include *Q. alba*, *Q. velutina*, and *Q. rubra* (Carvell & Tyron 1961). On the dry upper-third slopes and ridges, the commonly occurring *Quercus* species are *Q. prinus*, *Q. alba*, and *Q. coccinea*.

The forests of low terraces and well-drained bottomlands are composed of a mixture of *Fraxinus* species, *U. americana*, *C. occidentalis*, and *Q. macrocarpa* (Lorimer et al. 1994). *U. americana*, and *P. deltoides* are the most abundant species on low floodplains and along rivers. The number of species in the south is generally greater than in the north, as some southern species such as *Carya* species and *Betula nigra* extend northward into this region (Braun 1950).

In West Virginia, the most widespread species on lower slopes include *Q. alba*, and *Q. rubra* (Carvell & Tyron 1961). Bottomland hardwood forests in southern Illinois consist mainly of *P. deltoides*, *P. heterophylla*, *F. pennsylvanica*, *F. profunda*, *A. negundo*, *C. occidentalis*, *Carya* species, *Q. palustris*, *Q. macrocarpa*, *Q. shumardii*, *Q. bicolor*, *Liquidambar styraciflua*, *Plantanus occidentalis*, and *Salix* species (Hosner & Minckler 1963).

In general, the usual representatives of *Quercus-Carya* forest are second growth stands of scrubby *Q. velutina* and *Carya* on sandy soils, and *Q. alba*, *Q. velutina* and *Carya* species on clayey or intermediate soil types (Braun 1950). Unfortunately, very few areas of *Quercus-Carya* forest remain in undisturbed condition as much of the area has been grazed or cut.

Northern Hardwoods

This forest region extends from northern Minnesota and southeastern Manitoba, east through the upper Great Lakes region in southern Ontario to New Brunswick and south to New England (Braun 1950). Outliers of this forest region occur as far south as the Allegheny Mountains of Pennsylvania, Maryland, and West Virginia. *Q. macrocarpa* occurs in the northern hardwoods region in the northeastern half of Minnesota, southeastern Manitoba and adjacent Ontario, and the western part of Wisconsin. The topography is almost entirely depositional, with sandy outwash plains, till deposits, and many lakes.

Q. macrocarpa occurs throughout this forest region. The vegetation combines features from both the south and the north. The presence of trees, shrubs and herbs common in the southern deciduous forests indicate the migration of species from the *Quercus-Carya* forest. These species include *Q. alba*, *Q. macrocarpa*, *C. cordiformis*, *C. occidentalis* and *Rubus occidentalis*. *Pinus* species and other north-temperate species are also characteristic of this forest region.

Quercus species now dominate many areas that once supported extensive stands of *P. strobus*. Old *P. strobus*, which tower above the *Quercus*, still occur as remnants of the former forest. Common tree species occurring in *Quercus*-dominated areas include *Q. rubra*, *Q. alba*, *Q. macrocarpa*, *A. saccharum*, *T. americana*, *P. strobus*, *Fraxinus* species, *Juglans cinearea, U. rubra, B. papyrifera, C. cordiformis, A. rubrum*, and *Ostrya virginiana* (Braun 1950).

After clearcutting and burning in the 1800's, the former *Q. alba-P. strobus* forests in central Pennsylvania became dominated almost exclusively by *Q. alba* and *Q. velutina* (Abrams 1992). Increased *Quercus* species dominance in the mid-Atlantic region also occurred as a result of chestnut loss (attributable to chestnut blight) and fire suppression in *Pinus-Quercus* forests (Monette & Ware 1983, Stephenson 1986).

Western Mesophytic Forest Region

The western mesophytic forest region extends from northern Alabama and Mississippi northward to the southern boundary of Wisconsin glaciation in Ohio and eastern Indiana, and west to the southern boundary of Illinoian glaciation (Braun 1950). *Q. macrocarpa* occurs in two areas within this large region. One area is known as the Bluegrass region of north-central Kentucky and the other is in the Nashville Basin in central Tennessee. Both of these areas occur as islands within Oak savanna dominated regions.

The Bluegrass region has a rolling to hilly topography. The entire area is underlain by limestone covered by shallow soil. The region is characterized by old, widely-spaced trees and a carpet of *P. pratensis* (Braun 1950, Curtis 1959). *Q. macrocarpa* and *Fraxinus quadrangulata* are characteristic of the area. Other tree species present include *Q. muehlenbergii, Q. alba, Fraxinus americana, C. occidentalis, A. saccharum, J. nigra, U. americana, P. serotinia, C. ovata, Aesculus glabra*, and *Morus rubra* (Braun 1950).

The Nashville Basin resembles the bluegrass section of Kentucky in form, topography and some of its vegetational features (Braun 1950). The rolling parts, where the soil is deep, originally supported a forest of large trees. *Q. alba* and *Liriodendron tulipifera* are the principal species on the knolls, with *A. saccharum* most abundant on the slopes. Associated species include white *U. americana, Ulmus alata, J. nigra, Q. rubra, Q. muehlenbergii, Q. macrocarpa, C. ovata, N. sylvatica, P. serotinia*, and *L. styraciflua*

(Braun 1950, Curtis 1959). The lower slopes and flats between the knolls lack *Q. alba*, *L. tulipifera*, and *A. saccharum*. The higher hills, sheltered slopes support mixed mesophytic forest stands dominated by *Carya* species (Braun 1950).

1.5 Disturbance and *Quercus macrocarpa*

Oak savannas and woodlands are considered to be disturbance-maintained ecosystems (Chapman 1993, Leach 1995). Disturbance is defined as an action that quickly removes some living biomass but seldom affects all components of a community equally. Some components may be merely stressed, some unaffected, and others enhanced. The major causes of disturbance within *Quercus* ecosystems are fire, herbivory, disease, pests and human activity.

1.5.1 Pathogens and Pests

Q. macrocarpa often becomes susceptible to pathogens and pests when stressed (Wargo et al. 1983, Allen & Kuta 1994). Slight changes in the tree's growing environment such as grade changes, soil compaction around the root zone, injury, or changes in soil aeration may cause the tree to become vulnerable to insects and disease. It is usually a combination of more than one pathogen and/or pest that results in tree mortality (Wargo 1977).

Pathogens of Q. macrocarpa

Several pathogens commonly infect *Q. macrocarpa* trees, including the cotton root rot (*Phymatotrichum omnivorum*), strumella canker (*Strumella coryneoidea*), dothiorella canker and dieback (*Dothiorella quercina*), phoma canker (*Phoma aposphaerioides*), coniothryium dieback (*Coniothryium truncisedum*), oak wilt (*Ceratocystis fagacearum*), and Armillaria root rot (*Armillaria mellea*). However, only two have been found to potentially cause considerable damage to *Quercus* species: oak wilt and Armillaria root rot.

Oak Wilt (*Ceratocystis fagacearum*)

Oak wilt is widespread in the eastern and central United States, and is capable of causing considerable damage to *Quercus* trees in the central states (Rexrode & Brown 1983, Hiratsuka et al. 1995). It was first recognized as an important disease in 1944 in Wisconsin, where over half the *Quercus* species have been killed in localized areas. In other states, the fungus kills thousands of trees but this loss in only a fraction of the total oak timber volume. Oak wilt has also been found in Texas, which is well outside its main range (Dreistadt 1994).

All species of *Quercus* are susceptible to this vascular disease (Rexrode & Brown 1983). Generally, *Q. rubra* species are infected more frequently and succumb more readily than do *Q. alba*. However, *Q. macrocarpa* shows essentially the same symptoms as do *Q. rubra*.

The main period of infection is in the spring when new vessel wood is being formed. The leaves turn dull green or bronze, appear water-soaked, wilt, then turn yellow or brown. Heavy defoliation occurs in all stages of discoloration. These symptoms appear within a few weeks of infection in the crown of the tree. The disease progresses rapidly and some trees may die within one or two months after the appearance of symptoms. Most trees die within a year.

Armillaria Root Rot (*Armillaria mellea*)

Armillaria root rot affects many broadleaf trees and conifers worldwide (Dreistadt 1994, Hiratsuka et al. 1995). This pathogen is well established in *Quercus* forests, especially in areas subject to flooding (Wargo 1977), and is one of the most important diseases affecting conifers in the prairie provinces (Hiratsuka et al. 1995). This fungus infects and kills cambial tissue in the major roots and lower trunk (Dreistadt 1994). The first symptoms include undersized, discoloured leaves and premature leaf drop. Branches in the canopy die back until eventually the entire tree is killed.

During cool, rainy weather, clusters of mushrooms may form at the base of infected trees. Armillaria root rot also produces rootlike structures (rhizomorphs) which attach to the surface of roots. These rhizomorphs are capable of reaching up to 10 meters in length (Hiratsuka 1987).

Trees become infected with Armillaria root rot through root contact with infected plants or rhizomorphs attached to infected roots. Spores produced by mushrooms also disperse the fungus to dead stumps or other dead woody material. This fungus can develop slowly with symptoms not appearing until the fungus is well established. Armillaria root rot can survive for many years in dead or living tree roots (Dreistadt 1994).

Pests of Q. macrocarpa

A large number of insect species commonly affect *Q. macrocarpa* leaves, shoots, buds, seeds, twigs, and bark. Most insect species have little detrimental effect on *Q. macrocarpa* other than producing an unsightly appearance due to slight defoliation. However, the two-lined chestnut borer, forest tent caterpillar, and gypsy moth may have a large impact on the growth and health of *Q. macrocarpa* trees (Ives & Wong 1988).

<u>Two-lined Chestnut Borer (*Agrilus bilineatus*)</u>

The two-lined chestnut borer is the primary pest of *Quercus* species. It most frequently attacks *Q. macrocarpa*, *Q. palustris*, *Q. coccinea*, *Q. alba*, *Q. prinus*, *Q. stellata*, *Q. velutina* and *Q. virginiana* (Haack & Acciavatti 1992, Dreistadt 1994). It occurs from Newfoundland, west to the Rocky Mountains, and south to Florida and Texas.

Adult chestnut borers primarily attack both forest and urban-stressed *Quercus* trees (Dunbar & Stephens 1975, Wargo 1977, Haack & Benjamin 1982, Wargo et al. 1983, Dunn et al 1986, Haack & Acciavatti 1992, Allen & Kuta 1994, Dreistadt 1994, LeBlanc 1998). The first symptom of borer attack is the appearance of wilted foliage on scattered branches, which remains attached to the tree for several weeks or months before dropping (Haack & Acciavatti 1992). These branches die the following year. Usually, the crown is attacked in the first year with the remaining branches infested in the second and third years. Trees may be killed in the first year of an attack, but usually die after two or three years of successive borer infestation.

Gypsy Moth (*Lymantria dispar*)

The gypsy moth is one of the most notorious insect pests of hardwood tree species in the Eastern United States and Canada (Dreistadt 1994). It prefers hardwoods but will feed on several hundred species of trees and shrubs. A record 12.9 million acres of forest were defoliated by gypsy moth in 1981 (McManus et al. 1987).

The effects of defoliation by the gypsy moth vary depending on the condition of the trees, the amount of defoliation, and the number of years of consecutive defoliation (Hiratsuka et al. 1995). Healthy trees can usually withstand one or two consecutive defoliations of greater than 50% (McManus et al. 1987). However, trees weakened by previous defoliations or other stresses are frequently killed after a single defoliation. These weakened trees are also vulnerable to attack by other diseases and insect pests.

The gypsy moth was accidentally introduced into the United States from Europe by a French scientist in 1869. The first outbreak occurred in 1889, and by 1987 the gypsy moth had established itself throughout the Northeast (McManus et al. 1987, Ives & Wong 1988, Hiratsuka et al. 1995). It has not yet established itself in the Prairie Provinces of Canada or the central United States, but it may only be a matter of time before it does since it will feed on almost any species of tree and shrub (Ives & Wong 1988, Hiratsuka et al. 1995).

Forest Tent Caterpillar (*Malacosoma disstria*)

The forest tent caterpillar, a native insect found throughout the United States and Canada, attacks hardwood tree species (Batzer & Morris 1978, Dreistadt 1994, Hiratsuka et al. 1995). Outbreaks of this insect pest usually occur every 16 years in northern areas and typically last for 4-5 years (Ives & Wong 1988). *Quercus* species, *P. tremuloides*, *F. pennsylvanica*, *B. papyrifera* and *U. americana* are favorite tree species of the forest tent caterpillar (Batzer & Morris 1978). These caterpillars will also feed on ornamental shrubs and cultivated fruits and vegetables.

The forest tent caterpillar is capable of defoliating extensive areas of forest (Ives & Wong 1988). Light defoliation has little effect on tree growth, but two or more years of moderate to severe defoliations may cause considerable branch mortality. Trees are rarely killed, however.

Seed Insects

Larvae of a weevil species, *Curculio iowensisi*, attacks *Q. macrocarpa* acorns (Ives & Wong 1988). This species is found from eastern Canada to Saskatchewan and adjacent states in the U.S. (Hiratsuka et al. 1995). The adult weevils lay their eggs in the developing acorns. The larvae emerge from the ripe acorns and drop to the soil where pupation occurs more than one year later. The larvae eat all or part of the acorn contents, destroying the viability of the seeds. Occasionally, populations of this species are high in Manitoba and may destroy 10 to 20% of *Q. macrocarpa* acorns in one year.

1.5.2 Fire

Fire is an important natural disturbance in many ecosystems, and is a particularly common event in grasslands, savannas, and north-temperate forests (White 1983, Tester 1989). Indeed, prairies and oak savannas/woodlands are fire-maintained communities, since they are dependent on recurrent fires to prevent fuel buildup and to limit woody plant invasion (Leach 1995). In these communities, fuel (plant debris) often accumulates faster than it can decompose. Litter buildup decreases primary productivity and can alter species composition (Old 1969, Peet et al. 1975, Rice & Perenti 1978, Hulbert 1988). Fire consumes litter, stimulates the growth of fire-adapted species, and controls the growth and invasion of species that are not adapted to fire.

In the absence of fire, the climate and soils of the Midwest could support non-*Quercus* forests (Leach 1995). Throughout much of the Midwest, regular fires have historically maintained prairie and *Quercus* ecosystems (Sauer 1950, Curtis 1959, Bragg & Hulbert 1976, Grimm 1984). In the absence of fire, many *Quercus* stands are expected to be succeeded by more shade-tolerant tree species (Christensen 1977, Lorimer 1984, McCune & Cottam 1985, Nowacki et al. 1990). However, this successional pattern varies among regions and soil conditions, and is more common on mesic than xeric sites (Whitford & Whitford 1971, Abrams 1986, Host et al. 1987, McCune & Cottam 1985).

Influence of Fire on Quercus Forest Structure and Dynamics

Savanna *Quercus* species have a number of adaptations to recurrent ground fires, including a thick bark, resprouting ability, resistance to rotting after scarring, and the suitability of fire-created seedbeds for germination (Abrams 1992). Paleobotanical studies consistently reveal that *Quercus* pollen is associated with charcoal layers (Watts 1980, Abrams 1992).

Several factors affect the response of woody plants to fire, including plant size, season of the year, and fire intensity and duration. Few mature trees of most species are killed by light or cool ground fires, but hot fires will kill most species (White 1983, Reich et al. 1990). Mortality from cool fires varies considerably between tree species, particularly at the sapling and seedling stages. For example, a spring burn in central Wisconsin resulted in sapling mortality of 67 to 100% in *P. serotinia*, *B. papyrifera*, and *P. grandidentata*, but no mortality was recorded in *Q. ellipsoidalis* saplings (Reich et al. 1990).

Fires occur in the gallery forests of northeast Kansas approximately every 11 to 19 years (Abrams 1985). These fires generally burn into the forests from adjacent prairie regions (which burn every 2 to 3 years). Since gallery forests occur in stream channels and ravine bottoms, they are somewhat protected from fire. Gallery forests are also characterized by less fuel accumulation, lower fuel combustibility, faster litter decomposition, and higher relative humidity. These factors control the spread rate and fire severity of fires in the forest understory.

1.5.3 Herbivory

Quercus forests and savannas supply large amounts of food to ungulate herbivores, other vertebrates and various invertebrates. Herbivory undoubtedly has a great influence on the vegetation present (Leach 1995). While some forests and savannas are managed in order to sustain wildlife, others are degenerating due to heavy browsing (Alverson et al. 1994). *Quercus* forests and savannas are quite productive habitats, and much of the biomass produced is palatable to herbivores. *Q. macrocarpa* twigs and acorns are a significant component of the diets of deer, cattle, rodents, and birds (Goodrum et al. 1971, Severson & Kranz 1978, Darley-Hill & Johnson 1981, Uresk & Painter 1985).

Wild and Domestic Ungulate Herbivores

Q. macrocarpa is an important tree species in the management of white-tailed deer populations in the Black Hills of South Dakota (Severson & Kranz 1978). Preferred forage shrubs such as *P. virginiana* have declined in abundance, favoring the hardier *Q. macrocarpa* trees. *Q. macrocarpa* sprouts prolifically after its primary stem has been cut or damaged, but the nutritional and energetic value (proteins and crude fats) of young buds and twigs is so low that deer left to feed on *Q. macrocarpa* sprouts would eventually starve. Wildlife managers in the Black Hills selectively cut *Q. macrocarpa* trees to increase the amount of browse, but larger seed-producing trees are left untouched since the acorns produced are high in nutrients.

Pasturing in some areas has maintained savanna-like groves of open-grown *Quercus* trees (Leach 1995). The *Quercus* species themselves often fail to regenerate, however, since grazers often destroy seedlings and saplings (Alverson et al. 1994). *Q. macrocarpa* comprises about 12% of the diet of cattle in the Black Hills of South Dakota (Uresk & Painter 1985). Cattle consume *Q. macrocarpa* throughout the summer, and by September browse (trees and shrubs) comprises 37% of their diet. Similar results were obtained in central Oregon, where browse made up 47% of the diet of cattle when green grass was in short supply (Holechek et al. 1982, Roath & Drueger 1982).

While cattle may stimulate woody growth by disturbing the soil and herb layer (Dyksterhuis 1957), light pasturing may also help to preserve native herbaceous vegetation by keeping woody shrubs and tree saplings in check. Grazing also reduces fuel loads, with the result that fires are less frequent and of lower intensity. This in turn promotes woody vegetation development (Curtis 1959). Open Oak savannas are often maintained by moderate to heavy grazing, and succeed toward closed woodlands if grazing ceases (Chapman 1993).

Granivory

Acorns are a critical dietary item of blue jays, and this bird plays an important role in the long-distance dispersal of acorns (Darley-Hill & Johnson 1981). The North American blue jay (*Cyanocitta cristata*) is a *Quercus* acorn predator (Van Dersal 1940) that forages in the upper crowns of heavily masting trees. As the season progresses, acorns from the lower branches and fallen acorns may be taken. Jays remove the acorn cap by holding the bottom of the acorn with its feet and hammering the cap off with its bill. After removing the cap, the acorn is either hammered open and eaten or swallowed whole and cached later. One to five whole acorns are taken in a single feeding bout.

Upon arrival at the caching site, jays disgorge the acorns and deposit them on the ground in a pile. Acorns are subsequently moved to a nearby caching spot where they are dropped on the ground and covered with litter. In some cases acorns are hammered into the ground and then covered with litter. The process of covering acorns with debris or burying them may enhance germination and early growth by protecting the acorns from desiccation. Colonization of *Quercus* species from these jay caches may occur if a bird dies, fails to remember cache locations, or has surplus stores during mild winters.

Acorns are also dispersed short distances (10 to 30 m) by mice, squirrels and chipmunks (Johnson 1990). Squirrels hoard acorns in scattered clumps within a few hundred meters of parent trees (Crow 1988). Acorns are stored by burying them, which greatly increases their chance of successful germination. In non-masting years, blue jays and squirrels can entirely deplete the acorn crop. Bears, ungulates and various bird species will also feed opportunistically on acorns.

1.5.4 Human Activity

In North America, the loss of Oak savanna and woodland habitat has continued to this day. Significant impacts to ecosystem function and biodiversity are attributable to habitat degradation and fragmentation, air and water pollution, and climate change (Soule 1991).

Effects of Human Activity on Quercus Forest Structure and Dynamics

Oak savannas and woodlands often occur on sites of rolling topography that are desirable locations for residential homes (Chapman 1993). Riverine and lakeside ecosystems are subject to deforestation as they are often located near large urban centers. *Quercus* stands have also been cleared or fragmented during agricultural and industrial development. Active fire suppression has also resulted in the encroachment of later-successional species into oak savannas and woodlands.

Timber harvesting in *Quercus* stands may prove to be an enterprise consistent with sustainable forest management, but more research is needed to determine the appropriate harvesting methods (Leach 1995). Landowners often receive insufficient encouragement and technical support to manage their property for long-term values as opposed to short-term economic gain. The challenge is to find ways to ensure sustainable timber harvests, and to develop economic incentives for landowners that are consistent with maintaining ecosystem processes and biodiversity. Sustainable timber harvesting in *Quercus* stands may be compatible with habitat and biodiversity conservation, since these communities are often dependent on disturbance for their perpetuation. The challenge is to develop harvesting strategies that are compatible with the longevity, growth rate, and reproductive strategies of *Quercus* species.

1.6 Restoration and Management of *Quercus* Stands

A dramatic expansion of woody vegetation has occurred at the North American prairie-forest ecotone since European settlement in the mid-1800's (Abrams 1986). This expansion appears to be largely attributable to decreased fire frequency and intensity (Sauer 1950, Anderson & Brown 1983, Lorimer 1984, Abrams 1984). *Quercus* species dominated the ecotones forests (Rice & Penfound 1959, Curtis 1959), but these stands are gradually being invaded by more shade-tolerant and less fire-resistant tree species (Abrams 1986, Crow 1988). To reverse this trend, Oak savannas and woodlands are being aggressively restored and managed in the mid-western and central United States to maintain biological and landscape diversity (Leach 1995).

Common methods used for *Quercus* stand restoration and management include implementing a remedial fire regime to return the vegetation to a prescribed structure, the reintroduction of extirpated species, and the removal of exotic species (Leach 1995).

Management may also require the removal of drain tiles and drainage ditches, buildings, and pavement.

1.6.1 Girdling and Selective Cutting

Girdling

Girdling can be used to control clonal species such as *Populus*, *Prunus*, and *Acer* species (Chapman 1993). It is most effective in spring once the sap has begun to run and the cambial cells are filled with fluid. Girdling is more difficult and less effective at other times of the year. Managers may also combine girdling with herbicides: trees are girdled in the first year, and herbicides are used in the second year to kill the plant.

Selective Cutting

Although labor intensive, selective cutting is one of the most commonly used method to restore oak savannas (Chapman 1993). The technique varies from hand clipping to the use of chainsaws and chippers to remove large trees. This method has a number of drawbacks, including disturbance to the ground and problems associated with the disposal of cut debris. Debris may be disposed by scattering it in the understory (to be consumed by fire or decay organisms), by chipping and hauling it away (which is very expensive), or by burning it in piles (which sterilizes the soil and creates disturbed sites for exotic weed invasion).

1.6.2 Prescribed Burning

Prescribed burning is perhaps the single most important management tool for the restoration and management of oak savanna ecosystems (Tester 1989, Leach 1995). The method has been used since 1964 at the Cedar Creek Natural History Area of Minnesota to restore and maintain oak savanna (White 1983, Tester 1989).

The benefits of fire include: (a) allowing more light to the ground layer by top-killing some trees, saplings, and shrubs; (b) reducing the incidence of disease and/or infestation of insects; (c) maintaining habitat for certain wildlife; (d) removing accumulated debris from the ground layer; (e) providing regeneration opportunities for some species (Chapman 1993, McCarty 1993, Leach 1995). A possible negative impact of prescribed burning is the killing of desired species, particularly ground-dwelling invertebrates. Ill-timed fires may also kill desirable plants at vulnerable stages of their life cycle. Fires occurring prior to the growing season may stimulate the germination, growth, and seed production of annual plant species (White 1983). However, burning following annual plant emergence may be detrimental (Tester 1989). Clonal perennials generally respond well to fires regardless of their timing.

Prescribed Burning Techniques

In Missouri, two steps are taken to restore highly degraded oak savannas and woodlands: (a) reopening the midstory to increase light to the ground layer; (b) reinstating fire regimes (Leach 1995). Removal of most of the 30 to 50 year old understory trees is effective in increasing light penetration. Controlled burns are used to maintain an open midstory canopy, control woody resprouts, stimulate the expansion and reproduction of herbaceous plants, remove surface litter, and provide germination sites. Some undesired plants are more effectively controlled with herbicides, however. After initial clearing of the midstory and during the early stages of recovery, frequent prescribed burns are required. As the groundlayer recovers and new woody growth is suppressed, fire frequency can be reduced. Fires during the early restoration period tend to be light and spotty (McCarty 1993). Later in the restoration period, fire frequency decisions are made to balance fuel loading against advances in new woody growth. Excessive fuel accumulation increases fire intensity and may negate the positive effects of a prescribed burning strategy. In stands lacking a dense woody understory, restoration efforts can usually proceed simply by reintroducing fire.

To reduce very dense midstories, an expensive but effective approach is to hire crews to thin stands, treat stumps and burn the slash (McCarty 1995). Large machine-mounted choppers can be used to lower costs. An effective but potentially hazardous method is a prescribed hot fire that is timed to coincide with spring leafout in the spring. Such burns work best on steep terrain where convection columns magnify the effects. Autumn fires may achieve similar results. In severely degraded sites, species introductions may be required after a prescribed burn has taken place (Packard & Balaban 1994). Restorationists will often know before the first fire which areas will require remedial plantings.

Fire Effects in Oak Savanna

Historical and modern accounts indicate that fire suppression can significantly increase canopy closure within 20-40 years, although closure takes much longer on sandy ridgetops and on south-facing slopes (Curtis 1959). Fire suppression in fire-prone ecosystems increases canopy and subcanopy cover through invasion by fire intolerant species. In addition, litter layer and fuel loads increase and herb layer diversity declines (Chapman 1993). Increased tree cover results in higher understory humidity, lower soil temperature, lower wind speeds, and greater soil moisture retention.

Regular low-intensity fires are required to produce *Quercus* barrens that lack a shrubby understory (Chapman 1993). Annual burning kills smaller *Quercus* species (< 15 cm diameter) and keeps woody shrubs in check (Tester 1989). On severely degraded sites, cutting may be required to enhance the effects of annual burning (Chapman 1993). Once the desired community structure is attained, the fire interval can be relaxed to once every 2 to 3 years.

Restoring a densely forested area to oak savanna requires frequent and intense fires to kill the large diameter trees (Chapman 1993). Such fires will produce a scrub oak savanna. Subsequent burning will not kill the *Quercus* scrub and may increase stem density (Curtis

1959). Understory species diversity and biomass increases with increasing light intensity, and maximum abundance is achieved when the overstory density is considerably reduced (Bray 1958, Whitford & Whitford 1978, White 1983). The fire regime must be maintained to prevent shrub encroachment. For example, after four years without fire at a site in Minnesota, *C. americana* had largely grown back to its pre-burn density, height, and mass (Leach 1995).

The optimal timing of a fire will vary according to site quality and restoration stage (McCarty 1993). Dormant season burns (i.e. between late winter and mid spring) will leave some of the wet or frozen litter layers intact and thus protect the soil. Such fires 'top-kill' woody plants but do not scorch the dormant herbs and grasses (White 1983). While these fires are usually controllable due to the stable atmospheric conditions under which they typically occur, they can burn hotly when winds are strong (McCarty 1993). Standing snags are often too wet to smolder or catch fire.

Mid and late spring burns are known for their ability to top-kill woody plants and stimulate warm season grasses. Soil erosion is not a concern as green-up occurs rapidly following fire. Fires occurring as the buds are emerging or new leaves are unfolding may place an extra drain on carbohydrate reserves in competing woody plants. These fires can be very hot and are therefore very effective at removing midstory trees. Spring burns may also adversely impact the early spring flora.

Fall burns work well where light, leafy fuels are the only fire carrier. Burns at this time of year provide germination sites for fall-germinating seeds, and results in green autumn and early winter forage. Such fires also allow greater access to the fall seed crop by wildlife. Weather and fuel conditions during the fall are conducive to burning, and it is likely that the structure and function of oak savanna and woodland ecosystems are related to fall burning.

Examples of Use of Prescribed Burning

Prescribed burning in an oak savanna in central Minnesota at 1 to 3 year intervals was found to remove woody cover in the sapling and shrub layers, but had little effect on large canopy trees (< 30 cm diameter, White 1983). Grass and forb species increased in importance in this fire regime. Highest species richness occurred after two consecutive years of burning followed by two years without fire (Tester 1989). This increased species richness was attributed to the persistence of forest trees and shrubs combined with an increase in prairie species. Tree density and basal area decreased with increasing fire frequency, but most of the reduction occurred in the 5 to 25 cm trunk diameter classes. Compared to unburned areas, burned sites had consistently lower overstory diversity, less shrub cover, and higher frequency of grasses (White 1983).

Fire frequency and intensity were strong influences on two *Q. velutina* woodlands in northern Indiana (Chapman 1993). Infrequent, high intensity fires created an open overstory, a scrubby sapling layer of *Q. velutina* and *Q. alba*, and a high cover of herbaceous species. More frequent, low intensity fires were associated with higher canopy cover, higher density, lower basal area and lower herb and shrub cover.

Prescribed fire in open *Quercus* barrens in Northern Illinois resulted in no mortality or damage to large, isolated trees (Anderson & Brown 1983). However, higher fuel accumulations resulted in tree mortality in adjacent closed forest stands. Controlled fires may therefore be useful in restoring densely forested areas back to oak savanna. In central Wisconsin, prescribed burning also had positive effects on the structure of *Quercus* communities (Reich et al. 1990). Later successional species such as *Acer* were most negatively affected by fire, as the number and physiological performance of maple seedlings declined dramatically. Conversely, *Quercus* species showed greater net photosynthesis after fire and were much less sensitive to increases in water stress. Burning also resulted in increased cover of prairie and savanna species.

Prescribed burning is rarely undertaken in the northeast *Quercus* and eastern deciduous forests of North America (Johnson 1984). This is attributable to high human population density in the eastern United States and Canada, and less suitable burning weather in the region. Controlled burns in these stands, perhaps combined with shelterwood cutting, may encourage *Quercus* regeneration by increasing light levels and reducing understory competition.

1.6.3 Current Management Practices in Riding Mountain National Park

Currently, management practices such as monitoring permanent plots and prescribed burning are used to maintain the ecological integrity of forest communities in Riding Mountain National Park.

Establishment of Permanent Plots

Permanent plots can be established for long term monitoring of population and community dynamics (Chapman 1993). RMNP has established a one-hectare plot in the *Q. macrocarpa* stands to observe changes in community structure and composition, including seedling establishment and growth of advanced regeneration, canopy tree growth rates, productivity and the effects of climate change over time (Riding Mountain National Park 1998).

Fire Management

Prescribed burning is the single most important management tool in the restoration and management of oak savanna ecosystems (Tester 1989, Leach 1995). In RMNP, past fire suppression has resulted in an increased fuel load which may increase the risk of stand-replacing fires to which *Q. macrocarpa, F. pennsylvanica, A. negundo* and *U. americana* are poorly adapted. RMNP is currently in the process of updating fire history maps and evaluating fuel loads in different forest communities (Riding Mountain National Park

1998). These data are then linked with information essential for ecological monitoring and fire operations to determine a fire management program. The goal is to learn and support the timing, frequency and intensity of fires which will maintain natural evolving ecosystems representative of the Riding Mountain region.

Ongoing Research

RMNP is constantly involved in collaborative research and cooperative teamwork with universities, colleges, research institutes and government agencies (Riding Mountain National Park 1998). Research in areas such as vegetation management and ecosystem dynamics are encouraged to provide the necessary information to make informed decisions.

CHAPTER 2
OBJECTIVES

This study provides baseline ecological information on the location, community structure and composition, and forest successional dynamics of *Quercus macrocarpa* stands in Riding Mountain National Park. A detailed examination of vegetation-environment relationships is also provided. The specific objectives of the study were:

- to determine the location and areal extent of *Quercus macrocarpa* stands in the Park.
- to examine the population dynamics of *Quercus macrocarpa* stands, through an analysis of age and/or size class distributions.
- to summarize the floristic composition, community structure, and vegetation-environment relationships of *Quercus macrocarpa* stands.

CHAPTER 3

STUDY SITE DESCRIPTION AND EXPERIMENTAL DESIGN

3.1 Study Area

The *Quercus macrocarpa* stands enumerated in this study were located in Riding Mountain National Park, which comprises an area of 2973 km^2. Most of the Park occurs on top of the Manitoba Escarpment, a 300 m elevation rise that separates the lower Manitoba Lowlands from the Saskatchewan Plain (Riding Mountain National Park 1993). The Escarpment runs along the entire north and east margins of the Park and has a hummocky landscape with many small lakes and deeply cut stream channels. These channels cut through the Escarpment creating several north and south facing slopes along most of its length.

On the lowlands a variety of deciduous trees dominate the community. Characteristic trees include *Populus tremuloides*, *Ulums americana*, *Fraxinus pennsylvanica*, *Acer negundo* with some *Q. macrocarpa*, *Populus balsamifera*, and *Betula papyifera*. The warm, moist microclimate promotes a lush understory of herbs and shrubs.

On top of the Escarpment, most of the Park is covered with uneven aged *P. tremuloides-Picea glauca* associations of the boreal mixedwood forest. *Abies basamea* and *Q. macrocarpa* occupy north and south facing slopes respectively. *Pinus banksiana* occur on the well drained, east central portion of the Park while *Picea mariana* and *Larix laricina* grow in the wet bogs. Grassland remnants occur in the west portion of the Park.

The majority of *Q. macrocarpa* stands are found in the northeastern portion of the Park, on calcareous, well-drained alluvial soils and excessively drained south-facing slopes along the Manitoba Escarpment (**Fig. 3.1**).

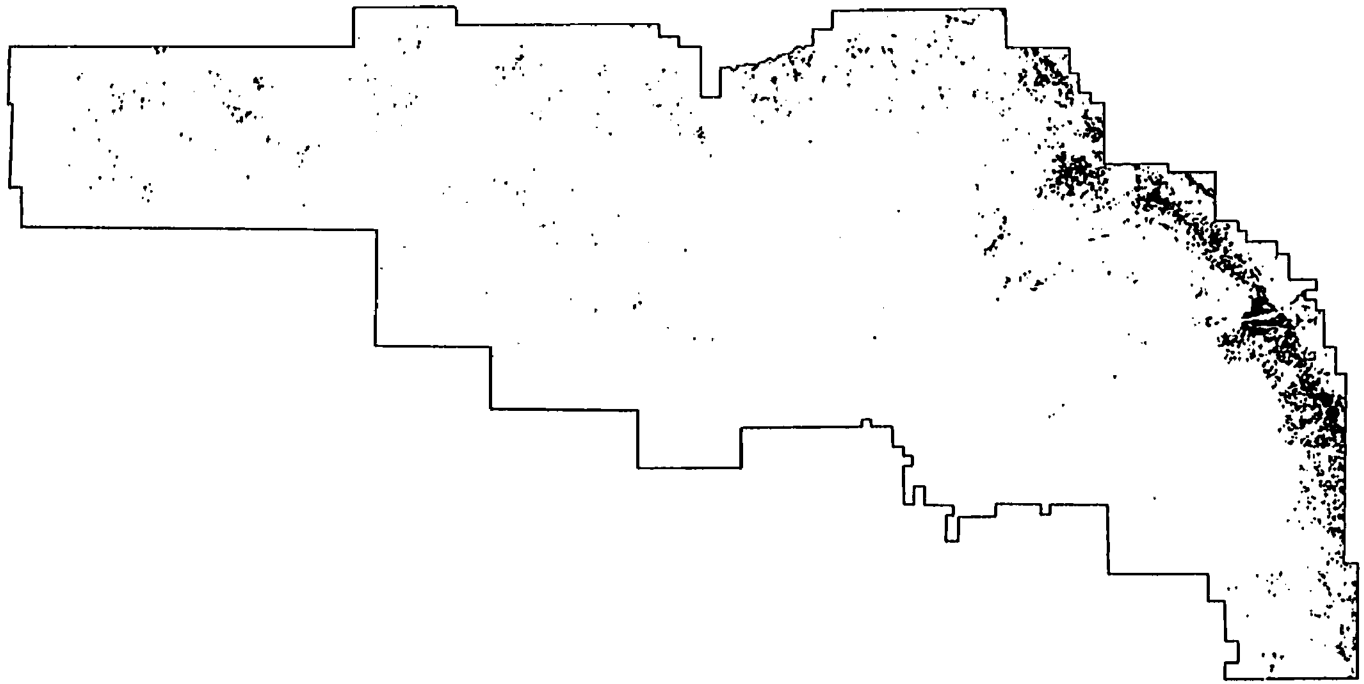


Figure 3.1 Riding Mountain National Park Quercus macrocarpa distribution map from classified LANDSAT TM data (modified from RMNP vegetation map, D.J. Walker). Shaded area = Q. macrocarpa dominated forest.

3.2 Climate

The climate of Riding Mountain National Park is characteristic of the continental climate of the Canadian prairies. Prevailing air masses from the south and southwest result in warm summers, while intrusions of arctic airmasses produce very cold winters. Turbulence generated by the Manitoba Escarpment along with the abundance of lakes and other wetlands, contribute to increased cloud and shower activity during the warmer months. Mean annual total precipitation is 47.6 cm. The warmest month is July (mean daily temperatures of 15.6°C), while January is the coldest (mean daily temperature of -20.6°C). RMNP has an average growing season of 72 days at Wasagaming but may vary considerably from year to year (Riding Mountain National Park 1998).

3.3 Data collection

3.3.1 Field Sampling

Q. macrocarpa stands were located using field reconnaissance, existing vegetation maps, and personal communication with park wardens. Vegetation and environment information was collected from 191 sample plots during the summers of 1998 and 1999 (**Fig. 3.2**). Each plot measured 10 x 10 m and was gridded into 5 x 5 m subplots to facilitate vegetation enumeration. Cover abundance estimates were obtained from each of the following six vertical canopies:

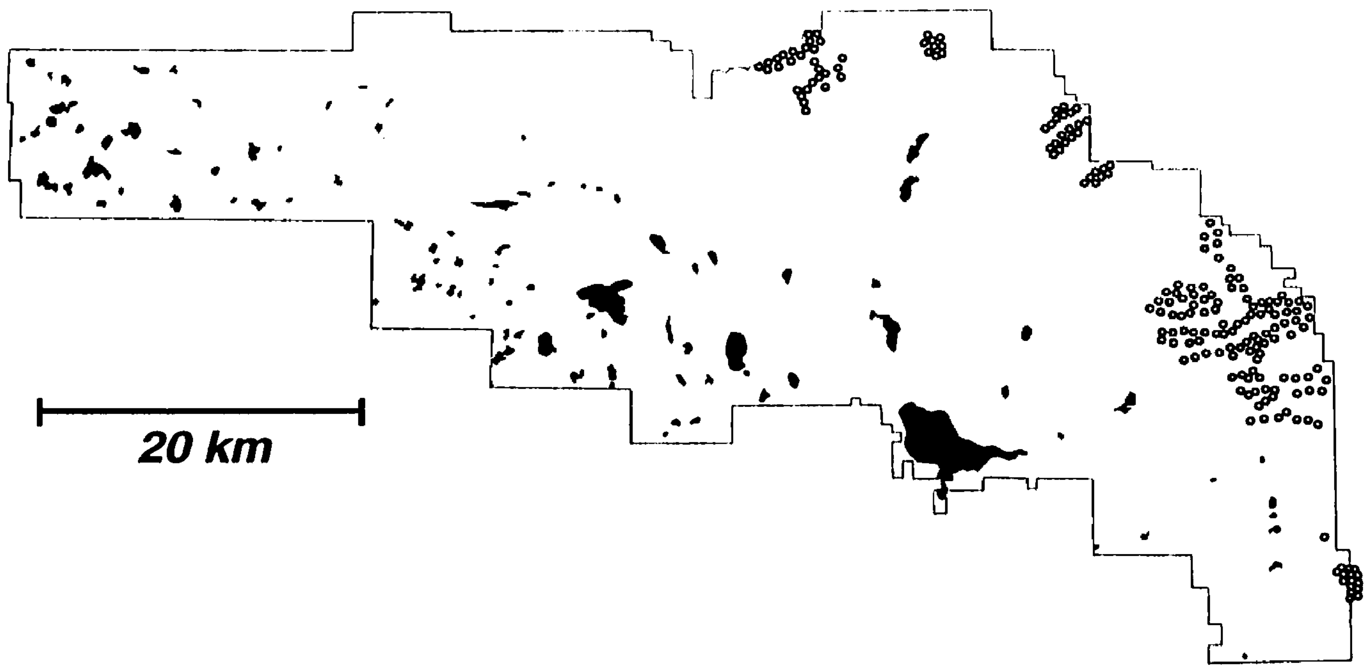


Figure 3.2. Riding Mountain National Park, with locations of the 190 bur oak study plots (open circles) sampled in the summers of 1998 and 1999.

Strata	Composition	Height (meters)
1	Canopy Trees	>15
2	Sub-Canopy Trees	10-15
3	Tall Shrubs and Low Trees	2-10
4	Low Shrubs and Saplings	< 2
5	Tree Seedlings, Graminoids, Forbs, Ferns and Fern-Allies	Usually <1
6	Bryophytes and Lichens	On forest floor

The following data were collected from each 10 x 10 m plot:

- Percent cover estimates for all species were obtained from each of the six vegetation strata. Cover was estimated to the nearest 5%. Low cover values were recorded as < 5%, 1% or < 1%.
- Diameter at breast height (DBH) was measured for all trees.
- A tree core was taken at breast height from the largest tree of each species using an increment borer.
- A soil core was taken from the center of each plot.
- Physical environmental factors, including slope, aspect, elevation and UTM coordinates were recorded.
- Detailed field notes were made at each site, including information on the surrounding vegetation, fallen trees, browsing intensity, evidence of past logging events, and evidence of pests-pathogens.

3.3.2 Species Nomenclature

A complete species list was compiled for the 1998 and 1999 field seasons (**Appendix 1**). Some graminoids were impossible to identify to species as they lacked reproductive parts. Species nomenclature follows Cody (1988) for vascular plants and Crum (1976) for mosses.

3.3.3 Minimum Stand Age

Minimum stand age was determined for each plot by increment coring the largest tree of each species at approximately 1.3 m height (DBH). In some stands the largest tree had a rotten center. In these cases the second largest tree in the stand was cored. Tree cores were mounted onto wooden dowels and sanded. Tree rings were then counted using a dissecting microscope. Since cores were taken at 1.3 m height the actual age of the tree was underestimated. Therefore, these counts should be considered minimum stand ages.

3.3.4 Soils

A soil pit was dug near the center of the plot and a representative soil core was collected. Each soil layer was measured and tested for carbonates. Soil cores were dried and kept in cold storage. Soil pH and conductivity were determined using an Accumet pH meter (model AR20). Soil texture (percent sand, silt and clay) was determined using the Bouyoucos hydrometer method and a Fisher Scientific Soil Hydrometer (model 14-331-58).

3.4 Data Analysis

3.4.1 Vegetation Analysis and Vegetation-Environment Relationships

The vegetation data set consisted of percent cover estimates of 113 species in 191 plots. The total cover for tree species was determined by summing the estimates from canopies one through four. Total shrub cover estimates were summed for canopies three and four. Percent cover values were log-transformed prior to multivariate analysis.

3.4.2 Delineation of Stand Types: Cluster Analysis

Cluster analysis is a hierarchical classification method that places individuals (*n*) into non-overlapping groups (*k*) based on a matrix of pairwise distances between plots (where $k<<n$). In this study, the minimum increase in error sum of squares (Ward's) clustering method was used to define the three stand types based on floristic composition.

The chord distance resemblance measure was used to determine the distance between plots. Chord distance uses proportional rather than absolute numbers of species, which normalizes the data and corrects for discrepancies in estimating percent cover between years. The cluster analysis was performed using the program HEIERCLUS in the statistical package SYNTAX-5 (Podani 1994).

3.4.3 Ordination of Stands: Correspondence Analysis

Correspondence analysis (CA) is an ordination method that summarizes the relationship between plots and species in a two-dimensional diagram. With this method the total chi-square ($\chi 2$) of the raw data matrix X (plots x species) is broken down into linear additive components:

$$\chi^2 = \sum_{i=1}^{k} \chi^2_i = X..(\sum_{i=1}^{k} R^2_i) \qquad (k = \text{MIN}\ \{p,n\}).$$

The R^2 values, which are squared canonical correlations, measure the relationship between the row and column variables in the data matrix. This partitioning of χ^2 is done by an eigenanalysis of the square symmetric matrix S:

$$S = UU' \qquad \text{where, } U_{ij} = [X_{ij}/\sqrt{(X_{i.}X_{.j})}] - [\sqrt{(F_{i.}F_{.j})}/F_{..}] \qquad (i=1 \text{ to } n, j=1 \text{ to } p)$$

The eigenvalues extracted from the square symmetric matrix S are the square canonical correlations ($\lambda_i=R_i^2$) which range between 0 and 1. These eigenvector elements are then used to derive component scores for both species and plots to create the ordination biplot.

The statistical program CANOCO (ter Braak 1987) was used to provide a graphical representation of the relationship as a biplot. Trends in species composition along the first CA ordination axis were summarized using the lowess (locally weighted scatterplot smoothing) method (Legendre & Legendre 1998).

3.4.4 Canonical Correspondence Analysis (CCA)

Canonical correspondence analysis quantifies the relationship between two sets of variables X (species data) and Y (environment). Specifically, CCA determines the degree to which the environmental data predicts the variation in vegetation composition. From this analysis, scores for variables and environmental factors are produced. The result is an ordination biplot which displays all variables and factors on the same diagram.

In this study nine environmental variables were used: slope, aspect (deviation from north), and seven soil variables (pH, conductivity, depth of organic layer, depth to C-horizon, percent sand, percent clay, and stoniness).

3.4.5 Physiognomic Profiles

Illustrative physiognomic profiles were created for the three *Q. macrocarpa* stand types delineated by cluster analysis (see Results). Each profile was based on density, relative frequency and percent cover values of dominant tree and shrub species. Topographic and edaphic variation were also used to depict the variation between stand types.

3.4.6 Summary Tables

For each of the three stand types the following summary tables were produced:

- Mean values for measured soil variables (pH, conductivity, depth of organic matter, and percent sand, silt and clay).
- Effective per plot species richness for canopy and subcanopy.
- Relative frequency of tree species over four vertical strata.
- Relative frequency and mean cover for all tree species.
- Mean basal area of tree species per plot.
- Mean tree density over five vertical strata per plot.
- Relative frequency and mean cover for all shrub species (frequency > 5%).
- Relative frequency and mean cover for common herbaceous, graminoid, and bryophyte species (frequency > 5%).
- Mean density and frequency of seedlings and suckers.

3.4.7 Effective Species Richness

Species richness is the total number of species present in a community. Effective species richness measures the probability that two randomly chosen individuals belong to the same species.

Effective species richness was summarized for the tree and understory canopy for each stand type. The understory canopy was further broken down into shrub and herb layers. Effective richness was computed as:

$$N = 1/\Sigma p_i^2$$

where p_i is the proportional mean cover of species i in a given stand type.

3.4.8 Forest Stand Dynamics

The frequency of tree species was used to infer successional trajectories for the three stand types and sub-type variants. For each of the six sub-types, the relative frequency of each tree species was determined for the upper three canopies. A size-class ordination (Bergeron & Dubuc 1989) based on correspondence analysis was used to summarize the data trends. Successional vectors were created by sequentially linking the coordinate positions of the three canopy strata for each sub-type.

CHAPTER 4
RESULTS

4.1 Delineation of Stand Types

Cluster analysis of the 191 sample plots was used to delineate three stand types, each with two sub-types (**Fig. 4.1**).

4.1.1 Stand-Type Summaries

I. Oak - Low Shrub ($n = 79$)

- *Two subtypes: I.A = very xeric (n = 38); I.B = xeric (n = 41):* These stands occur on nutrient-poor substrates, either on steep, excessively-drained, south-facing slopes or well-drained outwash plains. The soils are sandy to gravely and overlay carbonate pebbles or rocks. Carbonates often occur near the soil surface. Monodominant stands of scrubby, short-statured gnarled *Quercus macrocarpa* are characteristic of these sites. The understory is diverse and dominated by grassland species and low shrubs. Common shrub species include *Crataegus chrysocarpa* and *Viburnum rafinesquianum*. *Shepherdia canadensis*, which was not present in any other stand type also occurred in these stands. *Oryzopsis asperifolia*, *Carex* species, *Monarda fistula*, *Solidogo canadensis*, *Achillea millefolium*, and *Thalictrum venulosum* characterize the herb layer.

II. Oak - Tall Shrub ($n = 73$)

- *Two subtypes: II.A = subxeric (n = 50); II.B = submesic (n = 23):* These stands generally occur on low to moderate nutrient substrates, typically on old beach ridges and benches along the Manitoba Escarpment. The topography is slightly sloping to flat

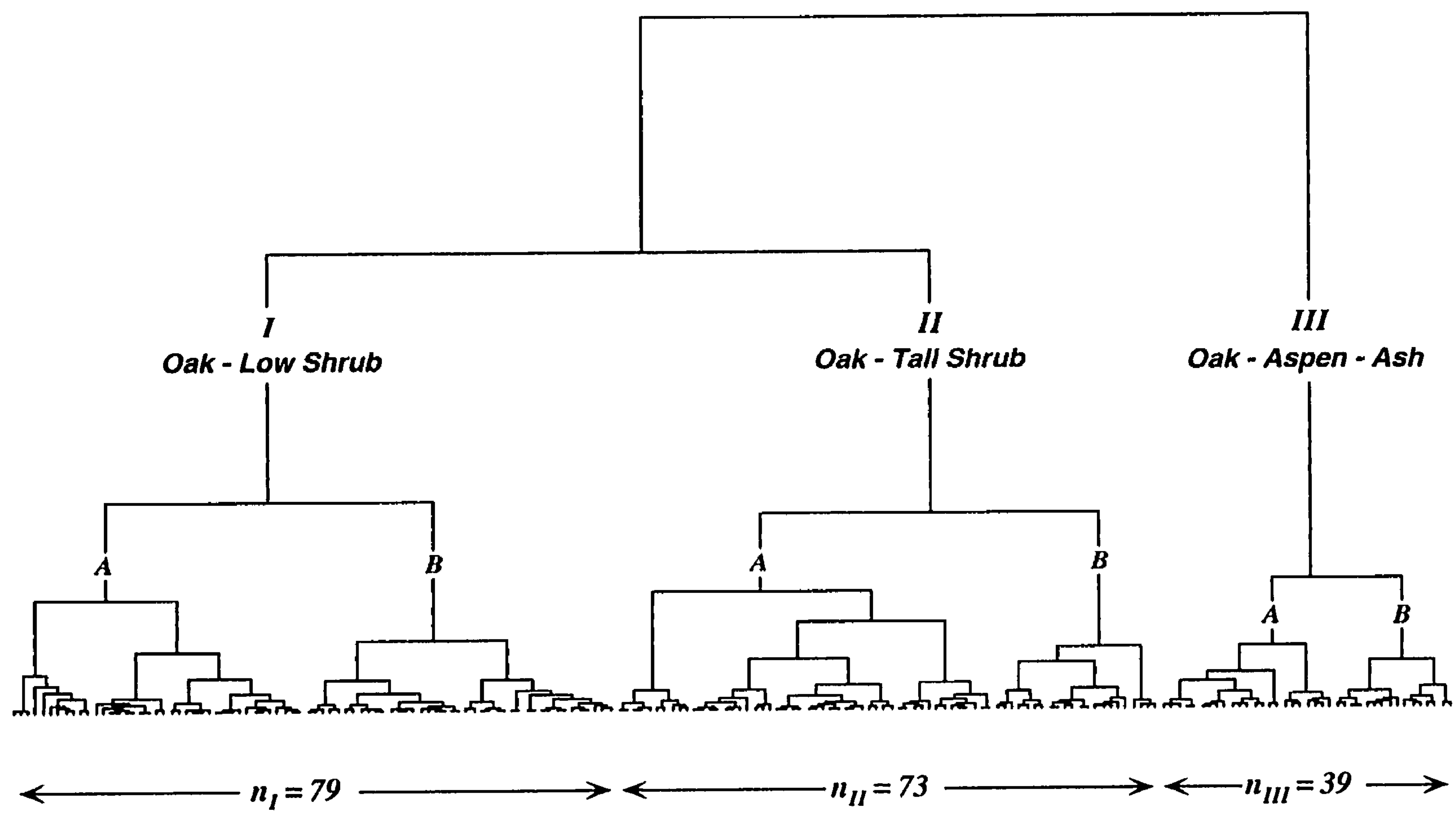


Figure 4.1. Cluster analysis dendrogram (Ward's method, chord distance, log-transformed data of 191 bur oak stands in Riding Mountain National Park. Three stand types (I-III) are delineated, each with two sub-type variants (A and B).

with a thin organic layer. *Populus tremuloides* and *Q. macrocarpa* are codominant in the canopy, while *Fraxinus pennsylvanica* is commonly encountered in the subcanopy. *Populus balsamifera* is occasional in the upper canopy, particularly in the mesic depressions of old beach ridges. The shrub layer in these stands is dominated by *Corylus cornuta*. Other commonly encountered shrubs include *Prunus virginiana*, *Cornus stolonifera*, and *Amelanchier alnifolia*. *Smilax herbacea*, *Maianthemum canadense*, *Disporum trachycarpum* and *Viola* species are common in the herb layer.

III. Oak - Aspen - Ash (n = 39)

- *Two subtypes: II.A = sub-hygric (n = 16); II.B = hygric (n = 23):* These stands generally occur on nutrient-rich substrates, typically in topographic depressions and lower elevations along the Manitoba Escarpment. There is often moderate organic accumulation. These are mixed stands of *F. pennsylvanica*, *Acer negundo*, *Q. macrocarpa* and/or *P. tremuloides*. *Ulmus americana* and *Betula papyrifera* are occasionally found in these stands. *P. tremuloides*, when present, occurs as very large trees that tower over the other species. *A. negundo*, *F. pennsylvanica*, and *Q. macrocarpa* are common in the lower canopy and regeneration layers. *C. cornuta* is the dominant shrub species, but *Acer spicatum* and *Viburnum trilobum* are also common. Rich woodland species are characteristic of the herb layer, including *Aralia nudacaulis*, *Matteuccia struthopteris*, *Pyrola asarifolia* and *Trillium cernuum*.

4.2 Vegetation-Environment Relationships

4.2.1 Environment

Q. macrocarpa stands in Riding Mountain National Park typically occur on shallow soils (mean depth to C-horizon = 13.7 cm) which are very sandy (mean sand content =

68.8%) (**Table 4.1**). The shallowest and coarsest soils occur in stand-type I, averaging 13.3 cm to the C-horizon and 71.2% sand. Soils are deepest in stand-type III (mean depth to C-horizon = 14.8 cm) and are somewhat less sandy (mean = 63.6%). These stands also had the highest clay content (mean = 14.6%).

Soil conductivity (an indicator of overall nutrient availability) ranges from 22 to 459 μS (mean = 149.7 μS), indicating low to moderate nutrient conditions across the range of *Q. macrocarpa* in the Park. Sandy, well-drained soils are normally low in conductivity. The lowest conductivity values were found in the xeric and sub-xeric sites (stand-types I and II) with averages of 146.4 and 142.4 μS respectively. More mesic sites (stand-type III) have a somewhat higher nutrient status (mean conductivity = 170 μS).

Depth of the organic layer (LFH horizon) ranges from 1 to 13 cm, with the greatest organic accumulation occurring in closed canopy stands of stand type III. Mean organic layer depth is 5.9 cm in stand type III, compared to 4.9 and 4.5 for stand types I and II respectively.

Slope ranged from 1 to 25%, with steepest slopes corresponding to the most xeric sites of stand type I. Exposure was also highest in the steepest sites, with an average deviation from North of 137°. More mesic sites (stand-type III) were flatter and less exposed. Most soils were somewhat stony (generally small pebbles), suggesting soils of alluvial origin.

4.2.2 Species Richness

Mean per plot (10 x 10 m) effective species richness values for the three stand-types are summarized in **Table 4.2**. Tree species richness is approximately equal to 1 in stand-type I, indicating that these are monodominant *Q. macrocarpa* stands. Tree richness increases to 2 in stand type II (codominant stands), and 4 in stand type III (mixed forest stands). Species richness in the understory shows the opposite trend: it is highest in stand types I

TABLE 4.1. Mean and range (parentheses) of edaphic, environmental and stand age variables.

	STAND TYPE							
	I		*II*		*III*		*All*	
	n = 79		*n = 73*		*n = 39*		*n = 191*	
	Mean	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*
pH	6.7	(5 - 8.3)	7.0	(5 - 8.4)	7.3	(5.5 - 8.4)	6.9	(5 - 8.4)
Conductivity (u S/cm)	146.4	(33.8 - 389)	142.4	(41.5 - 409)	170	(22 - 459)	149.7	(22 - 459)
Percent Sand	71.2	(40.6 - 92)	69	(32.5 - 92)	63.6	(37.4 - 85.5)	68.8	(32.5 - 92)
Percent Clay	11.5	(1.6 - 40.2)	12.3	(1.6 - 36.9)	14.6	(3.2 - 25.7)	12.5	(1.6 - 49.8)
Organic depth (cm)	4.5	(1 - 9)	4.9	(2 - 9)	5.9	(3 - 13)	5	(1.0 - 13.0)
Percent Slope	4.3		2.9		2.1		3.3	(1.0 - 25.0)
Aspect (deviation from North)	137.1		127.7		110.5		128	(0 - 352)
Stone (rank scale 1-5)	3.3		3.4		3.1		3.3	(1.0 - 5.0)
Depth to C horizon (cm)	13.3		13.5		14.8		13.7	(1.0 - 38.0)
Minimum Stand Age (years)	106	(35 - 295)	89	(22 - 299)	89	(35 - 193)	95	(22 - 299)

TABLE 4.2. STAND TYPE I. Effective per plot species richness for canopy and understory.

Stand-Type	*I*	*II*	*III*
Tree	1.07	2.00	4.02
Shrub	5.22	5.11	2.78
Herb	7.08	3.71	6.96
Understory	9.96	8.36	4.86

and II, and lowest in stand type III. Much of this difference is attributable to higher shrub richness in stand types I and II. Herb species richness is lowest in stand type II.

4.2.3 Correspondence Analysis (CA)

Stand Ordination

The CA ordination of the 191 plots (**Fig. 4.2a**) shows a clear separation of the three stand-types delineated by the cluster analysis. The high affinity between the classification and CA results confirm the robustness of the stand type delineation. The three stand types are well separated along the first ordination axis. Based on the distribution of the vegetation along this axis (**Figs. 4.2b-d**), it is interpreted as a complex soil-moisture gradient. Xeric sites are characterized by stand-type I, those of intermediate moisture by stand-type II, and mesic sites by stand-type III. The second CA axis is less well defined, serving mainly to separate the two subtypes of stand type III. It is therefore interpreted as a nutrient gradient (nutrients increasing from bottom to top).

Species Ordination

The species ordination (**Figs. 4.2b-d**) confirms the interpretation of the first axis as a complex soil moisture gradient. Species characteristic of xeric conditions such as *C. chrysocarpa*, *Arctostaphylos uva-ursi*, *Schizachne purpurascens*, and *V. rafinesquianum* occur on the left side of the ordination. At the opposite end of the ordination are species characteristic of moist, shaded conditions, such as *A. spicatum*, *V. trilobum*, *M. struthopteris*, *P. asarifolia*, and *Mitella nuda*. Species located near the center of the ordination figure such as *Q. macrocarpa*, *Fragaria virginiana*, and *P. virginiana* are either generalists or species that occur in intermediate moisture conditions.

The species ordination also confirms the interpretation of the second axis as a nutrient gradient. For example, *M. struthopteris* (a species indicative of moist, high nutrient sites)

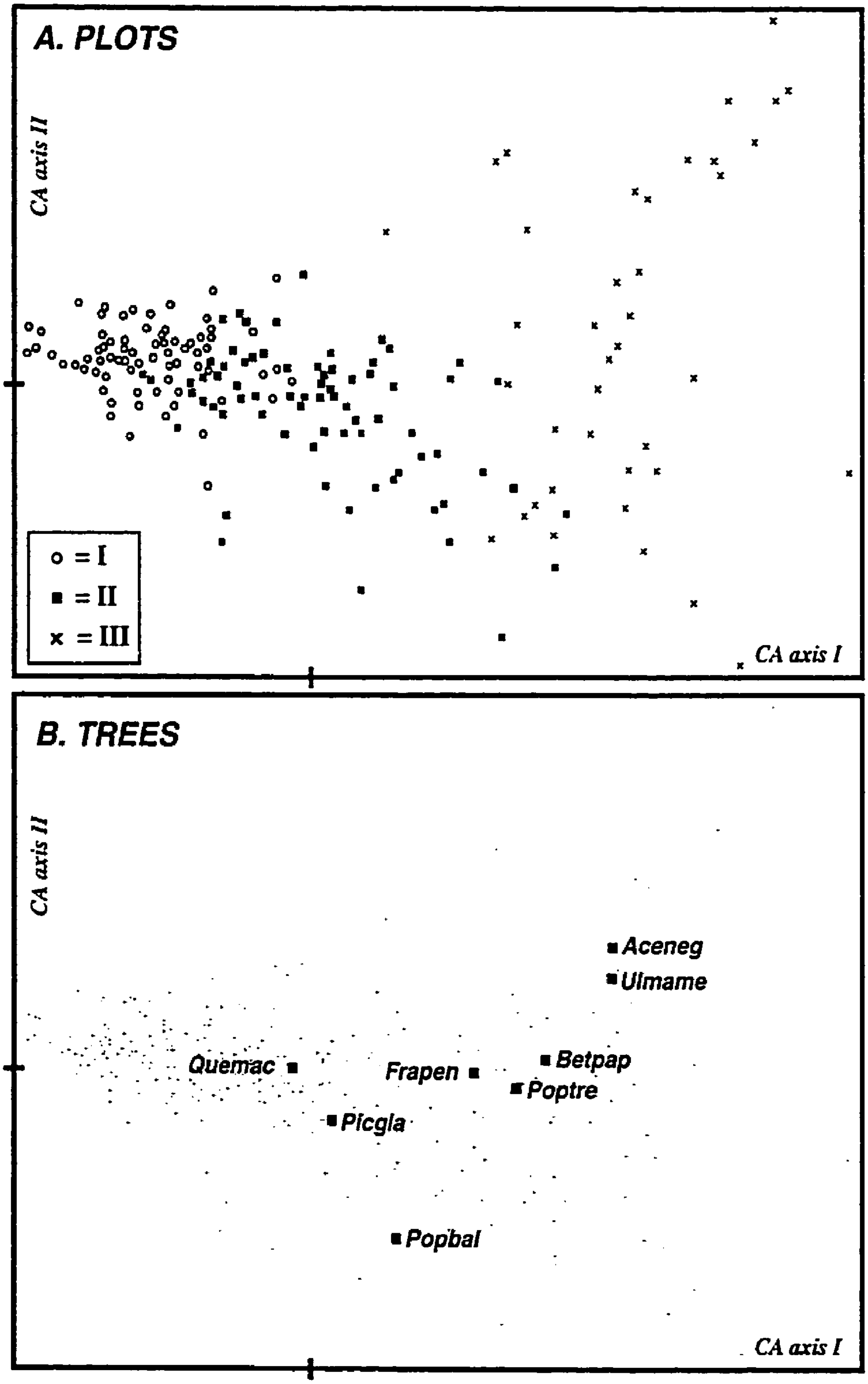


Figure 4.2. Correspondence analysis (CA) ordination of the 191 plots, based on species composition (log-transformed percent cover). A = Plots: symbols code for stand-types I - III. B = Trees: *Quemac* = bur oak; *Picgla* = white spruce; *Popbal* = balsam poplar: *Frapen* = green ash; *Poptre* = trembling aspen; *Betpap* = paper birch; *Ulmame* = elm; *Aceneg* = Manitoba maple. Eigenvalues: $\lambda_1 = 0.303$ (10.1%), $\lambda_2 = 0.151$ (5.0%).

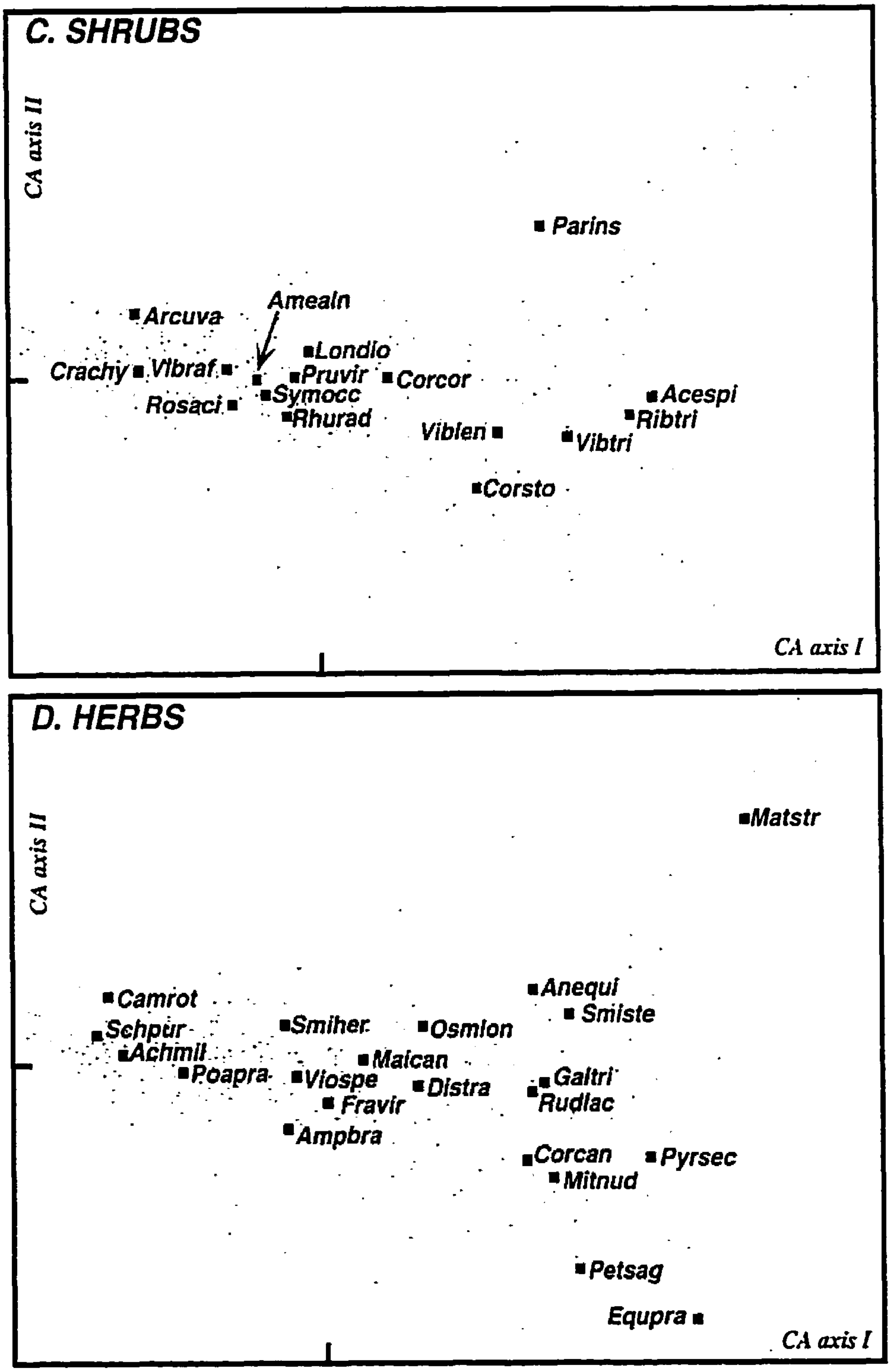


Figure 4.2 (cont'd). C = Common Shrubs: *Arcuva* = bearberry; *Crachy* = hawthorn; *Vibraf* = arrowood; *Rosaci* = rose; *Amealn* = saskatoon berry; *Symocc* = snowberry; *Rhurad* = poison ivy; *Pruvir* = chokecherry; *Londio* = honeysuckle; *Corcor* = hazelnut; *Corsto* = red osier dogwood; *Viblen* = nannyberry; *Vibtri* = highbush cranberry; *Parins* = virginia creeper; *Ribtri* = gooseberry; *Acespi* = mountain maple. **D = Common Herbs:** *Camrot* = bluebell; *Schpur* = oat grass; *Achmil* = yarrow; *Smiher* = carrionflower; *Poapra* = bluegrass; *Viospe* = violets; *Ampbra* = hog peanut; *Fravir* = strawberry; *Maican* = lily of the valley; *Distra* = fairybells; *Osmlon* = sweetcicely; *Anequi* = anemone; *Smiste* = solomon seal; *Galtri* = bedstraw; *Rudlac* = coneflower; *Corcan* = bunchberry; *Mitnud* = bishop's cap; *Petsag* = coltsfoot; *Pyrsec* = wintergreen; *Equpra* = horsetail; *Matstr* = ostrich fern.

occurs at the top, right of the ordination. *A. negundo* and *U. americana* are also found here. Species characteristic of moist sites of lower nutrient status, such as *Equisetum pratense* and *Petasites sagittatus*, occur on the bottom, right of the ordination.

Percent cover values of selected common species along the first ordination axis are summarized in **Appendix 2a-e**. *Q. macrocarpa* is present in all stands but peaks in the xeric sites and decreases as moisture availability increases. *P. tremuloides*, *F. pennsylvanica*, and *A. negundo* show the opposite trend: they are not present in the most xeric sites, but increase in cover and abundance with increasing soil moisture. Common shrub species that show peak abundance at the xeric end of the gradients include *V. rafinesquianum*, *C. chrysocarpa*, and *Rosa* species. *Rhus radicans*, *P. virginiana*, *C. stolonifera* and *Symphoricarpos occidentalis* peak at intermediate soil moisture levels, while *C. cornuta* and *V. trilobum* cover is highest at the mesic end of the gradient. Amongst the herbs, *Thalictrum dasycarpum* and graminoid (grasses and sedges) cover peaks at the xeric end of the gradient, *A. nudacaulis* cover is highest in intermediate sites, and *M. struthopteris* peaks in mesic sites. *Aster ciliolatus* and *F. virginiana* cover remains more or less constant along the gradient, indicating that they are generalist species.

4.2.4 Canonical Correspondence Analysis (CCA)

The moisture gradient from the unconstrained (CA) ordination was substantiated by the CCA results (**Fig. 4.3**). The CCA site ordination proved to be very similar to the CA ordination, indicating that the major trend in species-space has a strong underlying environmental (soil moisture) component, i.e. plant community composition is a good indicator of site conditions. Xeric sites (stand-type I), which occur on the left side of the ordination, are characterized by greater slopes, higher exposure (south-facing slopes), and more coarse-textured soils (higher sand content). By contrast, mesic sites (stand-type III), which occur on the right side of the ordination are characterized by greater soil organic matter accumulation, higher pH and conductivity, and more fine-textured soils (higher clay

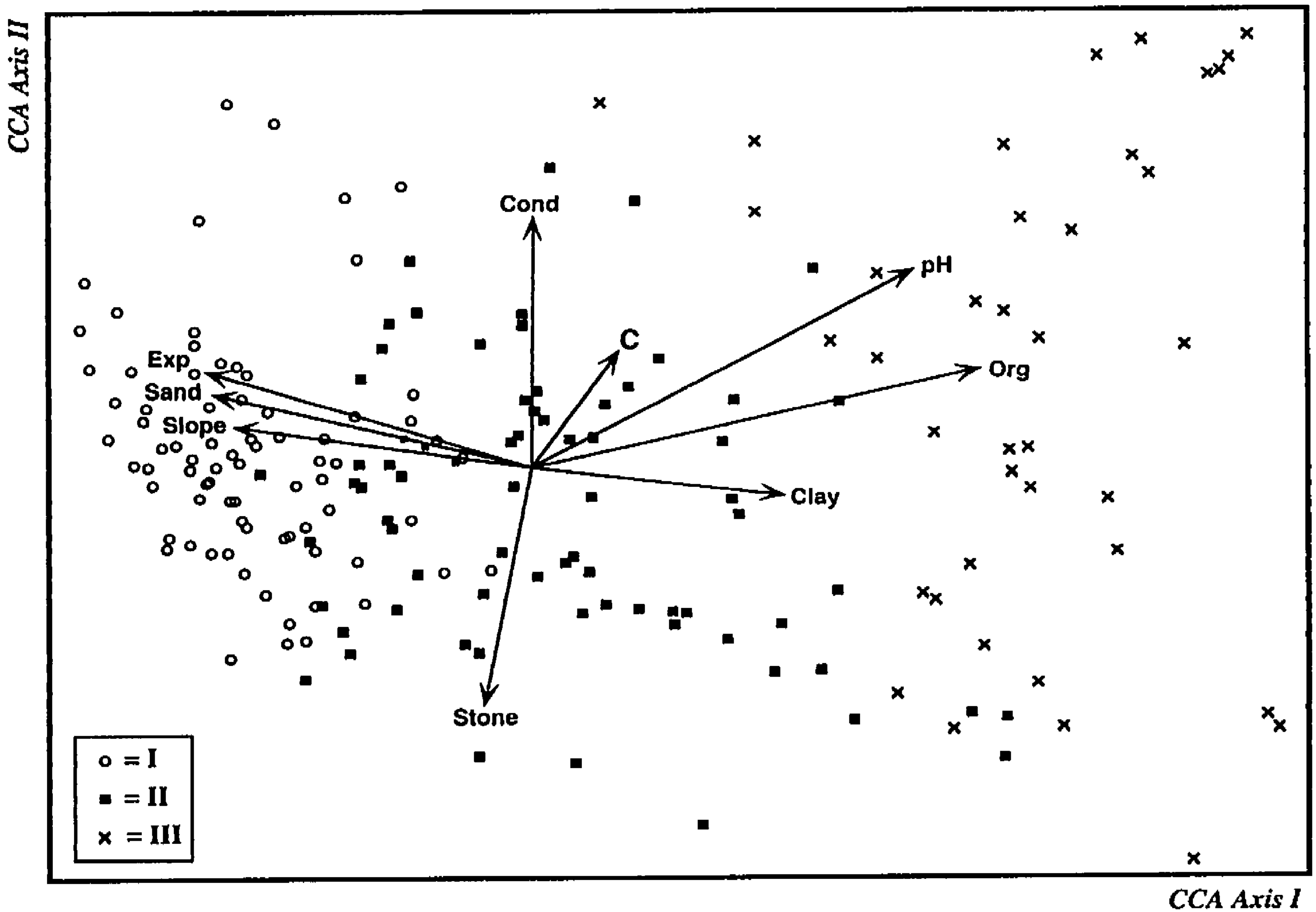


Figure 4.3. Canonical correspondence analysis (CCA) of 191 bur oak stands, based on plant species cover and constrained by nine environmental variables: **Exp** = exposure, direction from north; **Sand** = percent sand content of soil; **Slope** = percent slope; **Stone** = stoniness of soil, rank scale; **Cond** = soil conductivity; **C** = depth to soil C-horizon; **pH** = soil pH; **Org** = depth of soil organic layer; **Clay** = percent clay content of soil. Eigenvalues and canonical correlations: $\lambda_1 = 0.102$, $R^2 = 0.663$; $\lambda_2 = 0.026$, $R^2 = 0.640$. Amount of variance explained (ratio of constrained (canonical) to unconstrained eigenvalues = 0.199/1.427 = 14%.

content). The CCA ordination also confirms that species assemblages in the *Q. macrocarpa* stands are closely associated with environmental conditions. Tree diversity increases from stand type I to III as soil moisture and nutrient status increases. Understory diversity shows the opposite trend, decreasing along the moisture gradient. A more open canopy is characteristic of xeric sites, allowing more light to reach the forest floor and increasing understory diversity. By contrast, fewer species occur in the shaded understory of closed forest mesic stands.

4.3 Description of Stand Types

4.3.1 Stand Type I: Oak - Low Shrub (n = 79)

Stand Age

Q. macrocarpa in the upper canopy ranged in minimum age from 35 to 295 years, with a mean of 106 years (**Table 4.1**). Trunk diameter of these trees ranged from 11.6 to 35 cm, with an average DBH of 23.4 cm. The highly xeric environment of these sites severely limits the growth of these trees: the mean growth rate is 0.110 cm per annum (**See Chapter 5**). Trees growing on the steep south-facing slopes are typically very short-statured (< 3 m) and gnarled, but they can attain a very old age. Trees occurring on outwash plains and alluvial fans (more level topography) are usually slightly taller (3 to 7 m). Trees of this stand type attain a short, scrubby growth form with a short bole.

Edaphic – Environment

The majority of these stands occur on steep south-facing slopes, or on gravelly outwash plains at the base of the Manitoba Escarpment (eastern edge of the Park). The substrates are excessively to well-drained, with a thin organic layer (**Table 4.1**). The nutrient status is low (mean conductivity = 146.4 μS, range 33.8 to 389 μS). Sites with very high conductivity values were adjacent to fertilized agricultural land at the northern edge of the Park. Browsing intensity is high in open sites near trails, but is more moderate in stands located further away from trails.

Physiognomic Profile

Relatively open canopy, monodominant *Q. macrocarpa* stands are characteristic of this stand type (**Appendix 3a**). The trees are short statured on the steep south-facing slopes, but are slightly taller on more level topography. *P. tremuloides* and *F. pennsylvanica* may be very occasionally encountered in the subcanopy of less xeric sites. Shrub cover is low to moderate on steep slopes (sub-type Ia), but may be high on more level topography (sub-type Ib).

Vegetation

<u>Trees</u>

a) Canopy

Q. macrocarpa dominates all layers of the canopy in this stand type (**Appendix 4a-d**). Canopy cover is dominated by *Q. macrocarpa* (mean = 40%), with very low cover of *F. pennsylvanica, Picea glauca, P. tremuloides* and *Abies balsamea*. Density of *Q. macrocarpa* is very high in the third canopy (2-10 m), averaging 13 stems per plot. Poor growing conditions result in very few trees reaching the first or second canopy (> 10 m height). Mean basal area per plot is low, indicating that the trees are small in girth as well as stature. *F. pennsylvanica* and *P. tremuloides* occur very infrequently in the subcanopy of these stands. *P. glauca* rarely occurs as very large, old trees in the upper canopy. The effective tree species richness is only 1.07, reflecting the strong dominance of *Q. macrocarpa* (**Table 4.2**).

b) Regeneration

The regeneration layer (lower subcanopy and saplings) is strongly dominated by *Q. macrocarpa* (**Appendix 4d**). *Q. macrocarpa* in canopy 5 has the highest value with 17 seedlings per sample plot. *F. pennsylvanica* and *P. tremuloides* also occur as seedlings and saplings, but they rarely if ever reach the subcanopy or canopy layers. It therefore appears likely that *Q. macrocarpa* will persist and maintain its dominance in these stands, as it is most tolerant of the prevailing xeric conditions.

Understory

The understory vegetation is dominated by low shrubs, graminoids, sedges, and forbs. Effective species richness is 9.96, which is higher than both stand-types II and III (**Table 4.2**).

a) Shrubs

The shrub layer is dominated by *V. rafinesquianum* and *A. alnifolia*, with mean cover values of 18 and 27% respectively. *C. cornuta*, *C. chrysocarpa* and *P. virginiana* are also frequent but have lower cover values (**Appendix 4e**). *R. radicans*, *Rosa acicularis*, and *S. occidentalis* are also common, but they seldom exceed a height of 0.5 m. *A. uva-ursi*, a rare species in the Park, is very occasionally encountered on very xeric, steep south-facing slopes. Effective species richness of the shrub layer is 5.22, which is similar to stand type II but higher than stand type III (**Table 4.2**).

b) Forbs and Graminoids

Herbaceous diversity is high in these sites, which is probably attributable to high light levels (a very open canopy). A number of grasses and sedges dominate the herb layer. *Carex peckii* and *C. pensylvanica* are present in every site, with an average cover of 9% (**Appendix 4f**). *O. asperifolia*, *Schizachne purpurascens*, *Poa pratensis* and *Elymus* *canadensis* are commonly present. Characteristic forb species include *M. fistula*, *Lysimachia ciliata*, *A. millefolium*, *Lathyrus ochroleucus*, *F. virginiana*, *A. ciliolatus*, *Apocynum androsaemifolium* and *Agastache foeniculum*, many of which are characteristic of grassland ecosystems.

c) Cryptograms

Cryptogram cover is low in these xeric sites. *Brachythecium* and *Mnium* species were most frequently encountered, usually growing on dead wood.

Subtype Variants

Subtype Ia: Highly Xeric ($n = 38$)

These stands typically occur on very steep, south-facing slopes or on flat outwash plains. The driest sites occur on the Packhorse, Gorge Creek, and gravel pit trails where stands attain a savanna-like appearance with sparse, open-canopy *Q. macrocarpa* cover. All layers of the stand type are dominated by *Q. macrocarpa* (**Appendix 4g**). These trees are extremely short and have a gnarled growth form. The understory is dominated by sedges, grasses and low shrubs.

Regeneration in these stands is very high: on average, there were 18 *Q. macrocarpa* seedlings and suckers per plot (**Appendix 4i**). Suckers were often abundant, and were usually growing from the root collar of *Q. macrocarpa* trees that had been browsed or fallen over. Seedlings were less common. This high degree of regeneration, together with a lack of other tree species, suggests that these stands are self-replacing.

Subtype I.B: Xeric ($n = 41$)

These stands are typically found on moderate slopes or flat areas which are slightly less xeric than subtype Ia. Such stands are common along the Oak Ridge Trail, in the Vermillion River area, and along the North Escarpment Trail. The trees are slightly taller and have a straight bole, and do not take on the extreme gnarled appearance characteristic of trees in extremely xeric sites (subtype Ia). These stands are dominated by *Q. macrocarpa*, but very rarely a tall *P. glauca* may occur in the upper canopy. *F. pennsylvanica* and *P. tremuloides* are rarely encountered in the subcanopy (**Appendix 4h**). Shrubs dominate the understory with less herbaceous cover than the highly xeric sites.

Regeneration in these stands is very high: there is an average of 15 seedlings and suckers per plot (**Appendix 4j**). Regeneration of other tree species is poor, suggesting that *Q. macrocarpa* will maintain its dominance in these stands.

Discussion

These open, savanna-like stands of *Q. macrocarpa* occur on xeric substrates. Stands with similar structure and species composition occur in the northwestern portion of the *Q. macrocarpa* range, where the species often dominates the upper-slope transition between aspen parkland and the mixed grass prairie (Bird 1961, Scott 1996). Monodominant stands of *Q. macrocarpa* also occur in the Black Hills of western South Dakota and northeastern Wyoming, in a transition zone between ponderosa pine forest and the grasslands (Johnson 1990). Throughout much of the prairie region of the Midwest, *Q. macrocarpa* occurs on sandy plains and loamy slopes of south and west exposure (Curtis 1959, Abrams & Knapp 1986, Host et al. 1987, Johnson 1990, Hamerlynck et al. 1994). In Wisconsin, Kentucky, and western Iowa, it can be found as a dominant on well-drained soils of limestone or sandstone origin (Curtis 1959, Whitford & Whitford 1971).

Replacement in these sites by any other later successional species is unlikely, since no other trees are able to grow under such xeric conditions. Once established, *Q. macrocarpa* grows very slowly but can persist for hundreds of years. Although browsing is intense in some stands, the species responds by strongly suckering from the base.

4.3.2 Stand Type II: Oak - Tall Shrub ($n = 73$)

Stand Age

Canopy *Q. macrocarpa* ranged in age from 22 to 299 years, with an average age of 89 years (**Table 4.1**). These trees ranged in diameter (DBH) from 7.9 to 41.3 cm (mean = 23.5 cm). Growing conditions are slightly more mesic than in stand type I, resulting in a mean growth rate of 0.159 cm per year (see **Chapter 5**). *Q. macrocarpa* trees in these stands are relatively tall and usually have a straight bole. Canopy trees range in height from 15 m in submesic sites to only 5 m in subxeric sites.

Edaphic – Environment

The majority of these stands occur on old beach ridges and flat benches along the Manitoba Escarpment. Substrates are well to moderately drained, with some accumulation of organic matter (**Table 4.1**). Nutrient status is low to moderate (mean conductivity = 142.4 μS, range 41.9 to 409 μS), being highest in submesic sites and lowest in subxeric sites. Browsing intensity varies, but is highest near clearings and along trails.

Physiognomic Profile

This stand type is characterized by a relatively closed canopy dominated by *Q. macrocarpa*, sometimes in mixture with *P. tremuloides*, *F. pennsylvanica*, and rarely *P. balsamifera* (**Appendix 3b**). In submesic sites, large *P. tremuloides* or *P. balsamifera* may occur in the upper canopy. *F. pennsylvanica* occurs in the subcanopy of some stands. Tall shrubs, particularly *C. cornuta*, dominate the understory.

Vegetation

Trees

a) Canopy

Q. macrocarpa dominates all canopy layers, except in submesic sites where very tall individuals of *P. tremuloides* (or rarely *P. balsamifera*) may occur in the upper canopy (**Appendix 5a-d**). Canopy cover is dominated by *Q. macrocarpa* (mean = 36%). *F. pennsylvanica* and *P. tremuloides* occur in the lower canopy with mean cover values of 6%. *Q. macrocarpa* density is high in both the canopy and subcanopy layers, with averages of 3 and 7 stems per plot respectively. Density of *F. pennsylvanica* is highest in the lower subcanopy, with a mean of 1.5 stems per plot.

Mean basal area per plot for *Q. macrocarpa* is lower in the less xeric sites where other tree species (*P. tremuloides*, *F. pennsylvanica*) are able to establish. The effective tree species richness is 2.00, indicating stand codominance (**Table 4.2**).

b) Regeneration

Q. macrocarpa has the highest mean regeneration per plot, averaging about 6 stems per plot (**Appendix 5d**). Regeneration by *F. pennsylvanica* averages about 3 stems per plot, but few of these saplings reach the canopy layer. *P. tremuloides*, *A. negundo*, *A. balsamea*, *P. balsamifera*, and *U. americana* are very occasionally encountered in the regeneration layer.

<u>Understory</u>

A relatively dense cover of prostrate and tall shrubs characterizes the understory of these stands. The per-plot effective species richness of the understory is 8.3, which is intermediate between stand types I and III (**Table 4.2**).

a) Shrubs

C. cornuta and *A. alnifolia* dominate the shrub layer, with mean cover values of 38% and 11% respectively. *P. virginiana*, *C. stolonifera*, and *V. rafinesquianum* also occur at lower cover values (**Appendix 5e**). *R. radicans* and *R. acicularis* are common low shrubs, with mean cover values of 14% and 5% respectively. Effective species richness of the shrub layer is 5.11, which is similar to stand type I but higher than stand type III (**Table 4.2**).

b) Forbs and Graminoids

Herbaceous diversity is very low, with an effective species richness of only 3.71 (**Table 4.2**). The herb layer is almost entirely dominated by *A. nudacaulis*, with a mean cover of 22% (**Appendix 5f**). Other commonly encountered herbaceous species include *S. marilandica*, *M. canadense*, *S. canadensis*, *O. asperifolia*, and various sedges, but their cover is generally low.

b) Cryptograms

Cryptogram cover is low in these sites. *Brachythecium* and *Mnium* species were most frequently encountered, usually growing on dead wood.

Subtype Variants

Subtype II.A: Subxeric ($n = 50$)

These stands typically occur on well-drained benches and slight depressions along the Manitoba Escarpment. Such stands are encountered along the Thacker, Payne, and Oak Ridge Trails. The canopy is semi-closed. In most stands *Q. macrocarpa* dominates the canopy, but in some stands large individuals of *P. tremuloides* may occur in the upper canopy (**Appendix 5g**). The lower subcanopy is also dominated by *Q. macrocarpa*, but *F. pennsylvanica* and *P. tremuloides* may also be encountered. Tall shrubs dominate the understory.

Regeneration of *Q. macrocarpa* in these stands is moderate, with a mean of 6 seedlings and suckers present per plot (**Appendix 5i**). The high mean number of *A. balsamea* seedlings (mean = 2) is misleading, as this is the result of abundant regeneration in only one sample plot. *F. pennsylvanica* and *P. tremuloides* were each regenerating in about one-third of the stands. However, *Q. macrocarpa* dominates the regeneration layer suggesting that these stands are self-replacing.

Subtype II.B: Submesic (*n* = 23)

These stands are typically encountered in topographic depressions and benches at lower elevations near the base of the Manitoba Escarpment. They are most frequent in the northeastern corner of the Park along the Beach Ridges, Ochre River, South Escarpment, J.E.T. and Payne Trail systems. In these submesic stands, *Q. macrocarpa* grows taller and often exceeds 10 m in height. *F. pennsylvanica* and *Q. macrocarpa* frequently occur in mixture, often in association with *P. tremuloides* (**Appendix 5h**). *P. balsamifera* and *A. negundo* are more occasionally encountered. A dense tall shrub cover and low herbaceous layer characterize the understory.

Q. macrocarpa is regenerating in most stands, with a mean of 6 seedlings and suckers per plot (**Appendix 5j**). *F. pennsylvanica* regeneration is occurring in about half the stands, while *P. tremuloides* regeneration occurs in about one-third of stands. *A. balsamea, A. negundo, U. americana, P. balsamifera*, and *B. papyrifera* seedlings were also occasionally encountered.

Discussion

These semi-closed stands are codominated by *Q. macrocarpa* and *P. tremuloides* (occasionally *P. balsamifera*) in the canopy. *F. pennsylvanica* regeneration is high in some stands. Mixed *Q. macrocarpa-P. tremuloides* stands are characteristic of the aspen parkland region of Manitoba, but are uncommon elsewhere (Bird 1961). Succession from prairie to *P. tremuloides* is often slowed by limiting edaphic and climatic conditions. However, *Q. macrocarpa* is able to colonize more xeric sites to form mixed *Q. macrocarpa-P. tremuloides* stands. *Q. macrocarpa* also occurs adjacent to mixed-grass prairie in western South Dakota, often in mixture with *P. tremuloides* (Sieg & Wright 1996).

Stands of *Q. macrocarpa* (with or without *P. tremuloides*) with *F. pennsylvanica* in the understory occur in South and North Dakota (Wikum & Wali 1974). It has been hypothesized that *F. pennsylvanica* will eventually dominate these stands, but *Q. macrocarpa* is expected to persist as a stable associate (Johnson 1990). This successional trend is similar to stand type II in the Park.

In more mesic sites, *P. tremuloides* is often associated with *P. balsamifera* and (at higher elevations) *B. papyrifera*. *Q. macrocarpa* may also occur in these stands, particularly in topographically hummocky landscapes where drainage varies. Structurally similar stands occur in southern Michigan, *Q. macrocarpa* is restricted to slightly elevated ridges, while wet bottomland forest occurs in old glacial lakebeds and along drainage ways (Johnson 1990).

In the absence of fire, the climate and soils in the western range of *Q. macrocarpa* could support non-oak forests and be replaced by more shade-tolerant species (Christensen 1977, Lorimer 1984, McCune & Cottam 1985, Nowacki et al. 1990, Leach 1995). Therefore, without any disturbance these stands may become codominant stands of *Q. macrocarpa* and *F. pennsylvanica*. However, *Q. macrocarpa* is expected to remain a stable associate. The slow growth rate and suckering ability allow for *Q. macrocarpa* to remain in a stand for hundreds of years.

4.3.3 Stand Type III: Oak – Aspen - Ash (n = 39)

Stand Age

Q. macrocarpa range in age from 35 to 193 years, with a mean age of 89 years (**Table 4.1**). These trees ranged in diameter (DBH) from 5.9 to 42.0 cm, with a mean DBH of 22.4 cm. The more mesic growing conditions in this stand-type result in the highest growth rates of *Q. macrocarpa* (0.212 cm per year, **see Chapter 5**). *Q. macrocarpa* trees in these stands grow very straight and tall.

Edaphic – Environment

The majority of these stands occur at lower elevations at the base of the Manitoba Escarpment, mostly in the extreme northeastern portion of the Park. Substrates are moderately drained, and have organic accumulations ranging from 3 to 13 cm (**Table 4.1**). The nutrient status is moderate (mean = 170μS, range of 22 to 459 μS). Browsing intensity is generally low, but may be moderate to high along trail systems.

Physiognomic Profile

These stands are characterized by closed canopy containing a mixture of *Q. macrocarpa*, *P. tremuloides*, *A. negundo*, *F. pennsylvanica*, and/or *U. americana* (**Appendix 3c**). *P. tremuloides* dominates the upper canopy of many stands, with *A. negundo*, *F. pennsylvanica*, and *Q. macrocarpa* is the upper subcanopy.

Vegetation

<u>Trees</u>

a) Canopy

P. tremuloides dominates the upper canopy with a mean cover value of 22% (**Appendix 6a-d**). *Q. macrocarpa*, *A. negundo* and *F. pennsylvanica* have similar frequencies and densities in the subcanopy layers. However, *Q. macrocarpa* has the greatest cover of the three, averaging 17%. *U. americana* and *B. papyrifera* are occasionally encountered.

Mean basal area per plot is very low for *Q. macrocarpa*. *P. tremuloides* basal area is high, since individuals are generally very old and large. *F. pennsylvanica*, *A. negundo* and *Q. macrocarpa* have similar mean basal area values. The effective tree species richness is 4.02, which is the highest of the three stand types (**Table 4.2**).

b) Regeneration

Q. macrocarpa, *F. pennsylvanica* and *A. negundo* occur with approximately equal frequency and density in the regeneration layer (Canopy 5) (**Appendix 6d**). *P. tremuloides*, *B. papyrifera*, *U. americana* seedlings are also occasionally present.

Understory

Tall shrubs with a dense cover characterize these stands. The understory per-plot mean effective species richness is 4.8, which is the lowest of the three stand types (**Table 4.2**).

a) Shrubs

C. cornuta dominates the shrub layer and occurs at a mean cover of 54% (**Appendix 6e**). *A. spicatum* is found in about half the stands at moderate cover. *V. trilobum*, *Viburnum lentago*, and *A. alnifolia* may also be present. Low shrubs are uncommon. Effective species richness of the shrub layer is very low, which is attributable to the dominance of *C. cornuta*.

b) Forbs and Graminoids

Herbaceous diversity is high, with a mean effective species richness of 6.96 (**Table 4.2**). However, herb cover is low. *A. nudacaulis* occurs in most stands with a mean cover of 11% (**Appendix 6f**). *M. struthopteris*, which is a good indicator of moist, rich conditions, occurs in about one-quarter of the stands. *P. sagittatus*, *P. asarifolia*, *T. cernuum*, and *Anemone quinquefolia* are other characteristic species of mesic sites. Grass and sedge cover is very low.

c) Cryptograms

Cryptogram cover is low, but diversity in these stands is high. *Brachythecium*, *Mnium*, *Haplocladium*, and *Anomodium* species were encountered, usually growing on dead wood or as epiphytes on tree trunks.

Subtype Variants

Subtype III.A: Subhygric ($n = 23$)

These stands typically occur on moderately drained substrates at lower elevations and depressions along the eastern edge of the Manitoba Escarpment. Stands were encountered near the Vermillion River, Beach Ridges, South Escarpment and Payne Trails. *P. tremuloides* dominates the upper canopy, while *Q. macrocarpa* and *F. pennsylvanica* dominate the upper subcanopy. *B. papyrifera*, *U. americana*, and *A. negundo* are occasionally encountered (**Appendix 6g**). High cover of *C. cornuta* characterizes the understory.

Regeneration of *Q. macrocarpa* in this sub-type is moderate, averaging 4 seedlings and suckers per plot (**Appendix 6i**). *F. pennsylvanica*, *A. negundo* and *P. tremuloides* regeneration is also moderate. The relative frequency of *F. pennsylvanica* in the sapling layer is nearly twice that of *A. negundo* and *Q. macrocarpa*. It is possible that *F. pennsylvanica* may eventually increase in abundance in the upper subcanopy as the mature *P. tremuloides* die. However, because *Q. macrocarpa* is long-lived and is regenerating, it is also expected to persist in the upper subcanopy.

Subtype III.B: Hygric ($n = 16$)

These stands are typically found on moderately to imperfectly drained substrates at lower elevations and topographic depressions along the eastern edge of the Manitoba Escarpment. These stands occur near the Ochre River, South Escarpment Trails and near the eastern boundary of the Park at the Agassiz Ski Road. *F. pennsylvanica*, *A. negundo*, and *Q. macrocarpa* co-dominate the canopy or upper subcanopy (**Appendix 6h**). *P.*

tremuloides dominates the upper canopy of about half the stands. *U. americana* and *B. papyrifera* are occasionally present at low abundance. Tall shrubs (*C. cornuta* and *A. spicatum*) and *M. struthopteris* dominate the understory.

Moderate regeneration of *Q. macrocarpa, F. pennsylvanica, A. negundo*, and *P. tremuloides* is occurring in these stands (**Appendix 6j**). *U. americana* seedlings were occasionally present in low numbers. *F. pennsylvanica* and *A. negundo* seedlings were most frequently encountered, suggesting that they may increase in dominance over time. However, *Q. macrocarpa* will likely persist in the canopy, as the species is long-lived and is regenerating well.

Discussion

Q. macrocarpa, F. pennsylvanica, A. negundo and *P. tremuloides* are codominant species in this stand type. Stands with similar species occur as gallery forests in North and South Dakota, where *Q. macrocarpa* was found to grow in association with *F. pennsylvanica, A. negundo* and *U. americana* (Wikum & Wali 1974, Keammerer et al. 1975, Killingbeck & Bares 1978) in upland, mesic sites (Johnson et al. 1976, Reily & Johnson 1982). However, in these gallery forests *Q. macrocarpa* seedlings and young stems are uncommon (Johnson et al. 1976). Therefore, *F. pennsylvanica* will probably dominate these sites with *U. americana* and *A. negundo* as stable associates.

Gallery and bottomland forests in northeast Kansas and southern Illinois are experiencing a similar shift of dominant tree species (Hosner & Minckler 1963, Abrams 1986). Currently *Q. macrocarpa* and/or *Q. prinoides* is found in older forest stands (Abrams 1984, Knapp 1992, Hamerlynck & Knapp 1994). However, the oak species are not expected to progress to a climax. Instead, mixed hardwood stands of *F. pennsylvanica, A. negundo*, and *U. americana* tend to persist. Other eastern deciduous species tend to outcompete *Q. macrocarpa* seedlings in regenerating forests, as *Q. macrocarpa* is less tolerant of shade. In Riding Mountain, current regeneration of *Q. macrocarpa* appears to be sufficient in these stands, suggesting that it will persist but never dominate these richer, mesic sites.

In gallery forests further south, there is widespread potential for oaks to be replaced by more shade-tolerant species in the absence of fire (Christensen 1977, Lorimer 1984, McCune & Cottam 1985, Nowacki et al. 1990). However, this successional pattern varies among regions and soil conditions, and is more common on mesic than xeric substrates (Whitford & Whitford 1971, Abrams 1986, Host et al. 1987, McCune & Cottam 1985). Fires occur in the gallery forests of northeast Kansas approximately every 11 to 19 years (Abrams 1985). However, these forests have less vegetation growth (fuel accumulation) under the tree due to shading, lower combustibility of hardwood leaves concentrated at the tree base, faster litter decomposition at the base of the tree, and higher relative humidity.

In the absence of a stand-replacing disturbance (catastrophic fire), *Q. macrocarpa* will likely persist as a minor associate in this stand type. The long life of this species allows it to remain in a stand for hundreds of years.

CHAPTER 5

REGENERATION AND STAND DYNAMICS

5.1 Size Structure of *Quercus macrocarpa*

Size-frequency distributions by stand type of all *Quercus macrocarpa* trees enumerated in the study are presented in **Fig. 5.1**. In all stand types the size-frequency distribution is skewed, with greater representation in the smaller diameter classes. Stand type I has a very large number of individuals present while stand type III has the smallest number of individuals present. Very few of the trees achieve a diameter > 40 cm.

Since *Q. macrocarpa* size structure is skewed with a greater number of individuals in the smaller size class, this indicates continuous recruitment and a stable age-size structure. Not all of the young individuals survive however enough young saplings live allowing *Q. macrocarpa* to persist in each stand type. The high numbers of individuals in stand type I indicate dominance of bur oak while the small numbers of individuals in stand type III indicate it is present as a minor component of these stands.

All of the *Q. macrocarpa* trees maintain a diameter > 40 cm. However, all other tree species present had relatively similar diameters. The poor nutrient and moisture status in stand type I only allow for an extremely small increase in increment each year. The nutrient and moisture status in stand types II and III, although slightly higher, are still not rich enough to attain as large a girth as trees found on riverbanks or floodplains.

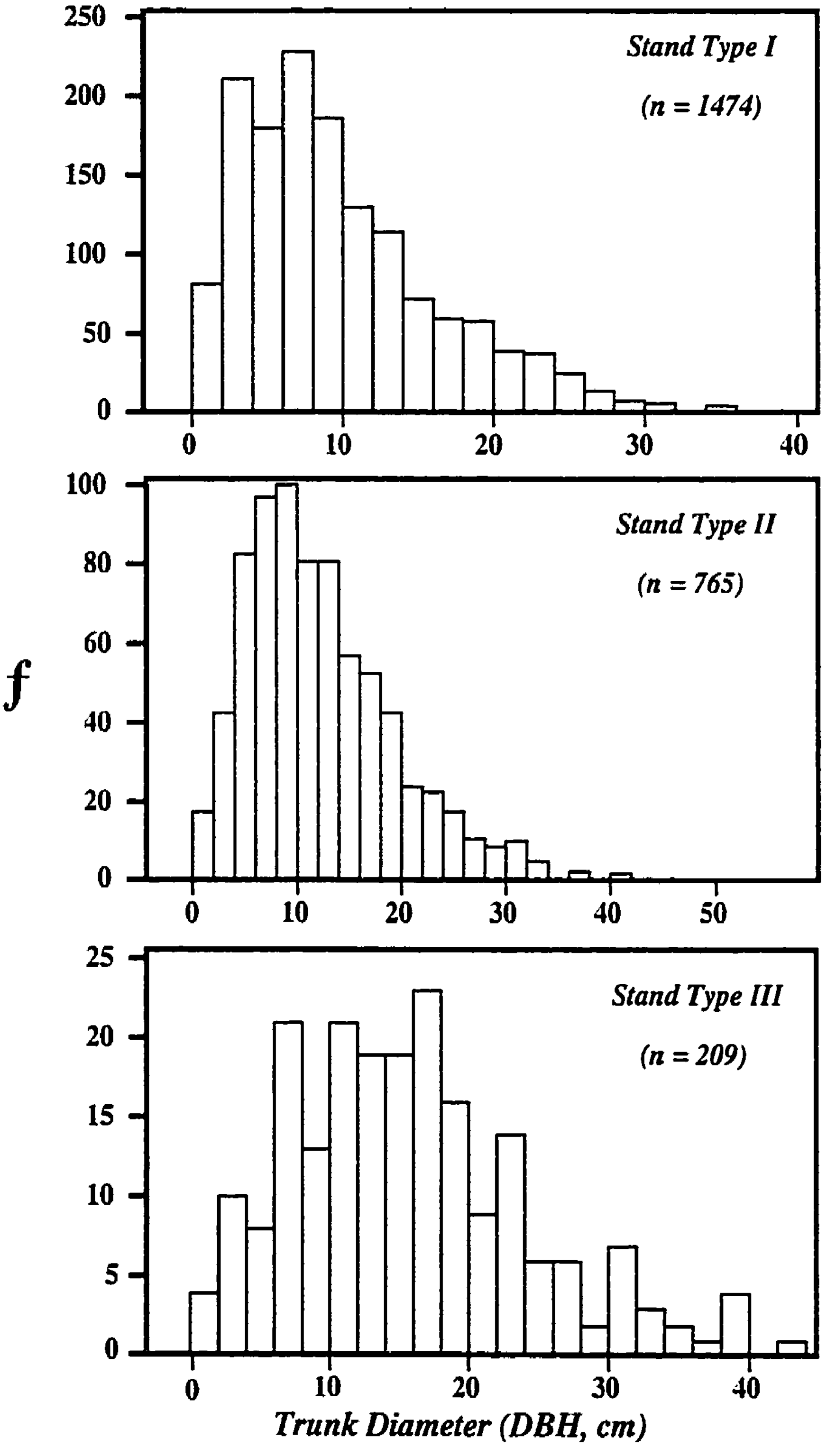


Fig. 5.1. Size-frequency distributions of stem diameters (DBH, cm) of bur oak in each of the three stand types.

5.2 *Quercus macrocarpa* Growth Rates

Within each stand type, the relationship between *Q. macrocarpa* age (tree core at 1.2 m height) and diameter (DBH, cm) was examined. For trees ranging in age from 40 to 200 years, the plots of age vs. DBH were linear (**Fig. 5.2**). This linear relationship was modeled by fitting the principal component to each scatterplot which measures the mean growth rate (increase in diameter growth per year) of established trees.

Growth rates varied in a systematic way, being lowest in the most xeric sites and highest in mesic sites. Trees occurring in the most xeric sites (stand type I) grow very slowly, with mean incremental diameter increases of only 1.1 cm every 10 years. Trees in stand type II grow somewhat faster, at 1.6 cm incremental diameter every 10 years. Greatest growth occurs in the most mesic sites (stand type III), with a mean incremental diameter increase of 2.1 cm every 10 years.

These results suggest that, although *Q. macrocarpa* is very drought-tolerant, its growth is limited by moisture availability. Sites with the highest moisture status (stand type III) had the greatest growth rate and sites with the lowest moisture status (stand type I) had the slowest growth rate.

5.3 Regeneration of *Quercus macrocarpa*

Q. macrocarpa is somewhat shade-intolerant, which limits regeneration in closed forest stands and in sites where shrub cover is high. As summarized below, recruitment is greatest in open, high light sites but is strongly limited in closed-canopy stands. This suggests that light, rather than soil moisture and nutrient availability, limits *Q. macrocarpa* recruitment in Riding Mountain National Park.

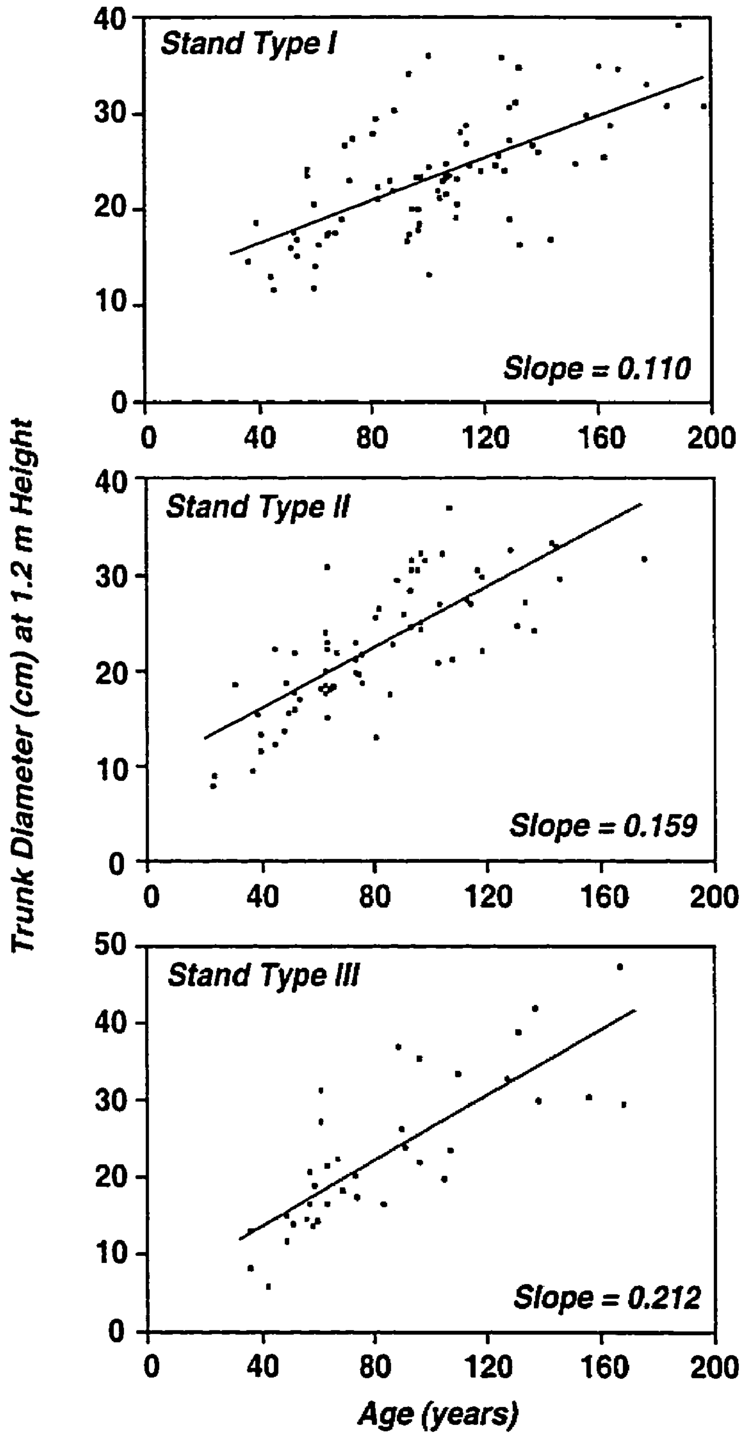


Figure 5.2. Relationship between trunk diameter at 1.2 m height (cm) and age (years) for bur oak in each of the stand types I-III. The fitted lines are principal components. Slope values are interpretable as growth rates (annual trunk diameter increment, cm).

5.3.1 Stand Type I (Oak – Low Shrub)

Q. macrocarpa regeneration in this stand type is high, as saplings were found in about 40% of plots (Canopy 4) (**Appendix 4a**). Large numbers of seedlings and sucker shoots in canopy 5 were also encountered with a mean of 16.92 per plot (**Appendix 4d**). However, the density of saplings was only 3.63 per plot. This is likely attributable to intense browsing, which results in the production of a high number of suckers from the root collar of the disturbed tree. Most of these are of poor quality and do not survive (Johnson 1990). Therefore, only 20% of seedlings and suckers recruit into the sapling layer. Even with this loss, *Q. macrocarpa* seedlings are very efficient users of water, and quickly develop a deep taproot (Weaver 1932, Crow 1988, Johnson 1990). They may live for several years even when intensely browsed, but remain short (> 0.5 m) due to the continuous cropping.

In these stands, the open canopy provides plenty of light for the shade-intolerant seedlings (Johnson 1990). No other tree species are able to colonize in these xeric sites due to the low nutrient, high light conditions. Without any competition, *Q. macrocarpa* will remain the only and dominant tree species in this stand type.

5.3.2 Stand Type II (Oak – Tall Shrub)

Regeneration of *Q. macrocarpa* in this stand type is low to moderate. Saplings (canopy 4) were encountered in 15% of the plots (**Appendix 5a**). Seedlings (canopy 5), with a mean value of 6.38 per plot were found at a greater density than saplings which had a mean value of 0.42 per plot (**Appendix 5d**). *Q. macrocarpa* is regenerating well but seedlings rarely reach the sapling stage due to strong interspecific competition for light.

These sites are less limited by water, but are dominated by tall shrubs and have a more closed canopy. Lower light levels therefore appear to be limiting recruitment of *Q. macrocarpa* into these stands: a dense shrub cover may be particularly detrimental to *Q. macrocarpa* recruitment (Johnson 1990, Hamerlynck & Knapp 1994). *Fraxinus pennsylvanica*, which is more shade-tolerant but less drought-tolerant than *Q. macrocarpa*, is often present in the regeneration layer of more mesic sites (sub-type IIb). *F. pennsylvanica* had a total of 6.78 seedlings and suckers per plot while *Q. macrocarpa* had a total of 6.08 in stand type IIb (**Appendix 5j**). This indicates that *F. pennsylvanica* may become a codominant tree species in the next generation.

5.3.3 Stand Type III (Oak – Aspen – Ash)

Q. macrocarpa regeneration in this stand type is low, as saplings (canopy 4) were present in only 8% of plots (**Appendix 6a**). Seedlings (canopy 5) were found at a density of 3.74 per plot while saplings had a density of 0.08 per plot (**Appendix 6d**). Other tree species, *Acer negundo*, *F. pennsylvanica* and *Populus tremuloides* had higher densities than *Q. macrocarpa* in canopy 5 with values of 5.64, 3.92 and 3.74 respectively. Both *A. negundo* and *F. pennsylvanica* also had higher sapling densities with values of 0.36 and 0.85. *P. tremuloides* had a similar sapling density as *Q. macrocarpa* with a value of 0.05. Both *Q. macrocarpa* and *P. tremuloides* are shade intolerant, therefore recruitment into the sapling layer is limited by light availability.

These stands are characterized by a dense, closed canopy and high cover of tall shrubs. The deeply shaded conditions strongly limit *Q. macrocarpa* recruitment, favoring more shade-tolerant species such *F. pennsylvanica*, *A. negundo* and *Ulmus americana* instead.

As the larger, older trees die and fall over, canopy gaps created favor the establishment of *Q. macrocarpa* and other less shade-tolerant tree species (*P. tremuloides*) that can germinate and grow quickly under high-light conditions (McCarty 1993). Once established as a sapling, *Q. macrocarpa* is able to persist and will eventually reach the canopy (Davis 1998).

5.4 Vegetation Dynamics of *Q. macrocarpa* Stands

Size-class ordination analysis is an effective method for summarizing overall trends in forest dynamics under the assumption that there is no catastrophic disturbance. This model also assumes that species composition and abundance in the subcanopy and sapling layers are indicative of future forest canopy composition. In the present model, three canopy layers were used: canopy-subcanopy (layers 1 and 2, > 10 m height), lower subcanopy (layer 3, 2 – 10 m), and saplings (0.5 – 2 m). Six trajectories were produced, one for each sub-type for all stand types. Relative frequency values of the major tree species were used in the analysis. The resulting ordination (based on correspondence analysis) is shown in **Fig. 5.3**. Vectors close to tree species names on the ordination indicate a stand type dominated by that tree species.

5.4.1 Stand Type I (Oak – Low Shrub)

Both sub-types of this stand type are undergoing little change in terms of their canopy-subcanopy dynamics. Successional vectors are short and non-directional, suggesting that these stands are self-replacing (**Fig. 5.3**).

Q. macrocarpa regenerates well in these sites (**Fig. 5.4a**). Although slow-growing in these sites, *Q. macrocarpa* is a long-lived species that is highly tolerant of droughty conditions and high light levels. The species also undergoes extensive vegetative propagation (root collar suckers) in these xeric sites. Conditions are too extreme for other tree species.

These sites generally have low fuel loads. The highly xeric conditions are not suited for the growth of tall shrubs, and as a result the understory is dominated by low shrubs, herbs and graminoids. Such sites are characterized by light ground fires that burn at low temperatures (White 1983, Reich et al. 1990). *Q. macrocarpa* bark is fire-resistant (Johnson 1990), but trees will resprout if the above-ground portion is killed (Abrams

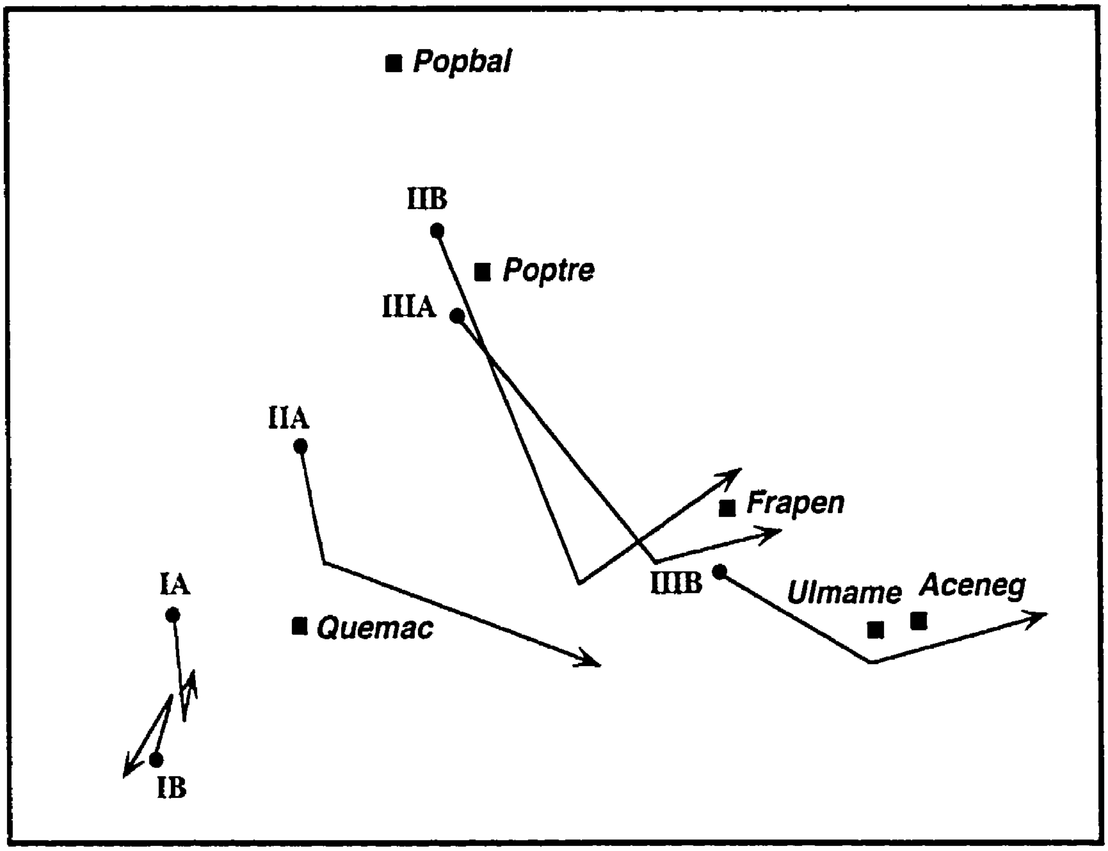


Figure 5.3. Successional trajectories for the three bur oak stand types and their subtypes. The successional vectors were obtained using size-frequency ordination analysis. Closed circles indicate relative stand-type locations based on current canopy composition. The direction and length of vectors indicate possible successional trends, based on composition in the subcanopy and advance regeneration (sapling) layers. Long vectors suggest possible changes in canopy composition, while short, non-linear vectors suggest that stands are self-replacing. Refer to text for details.

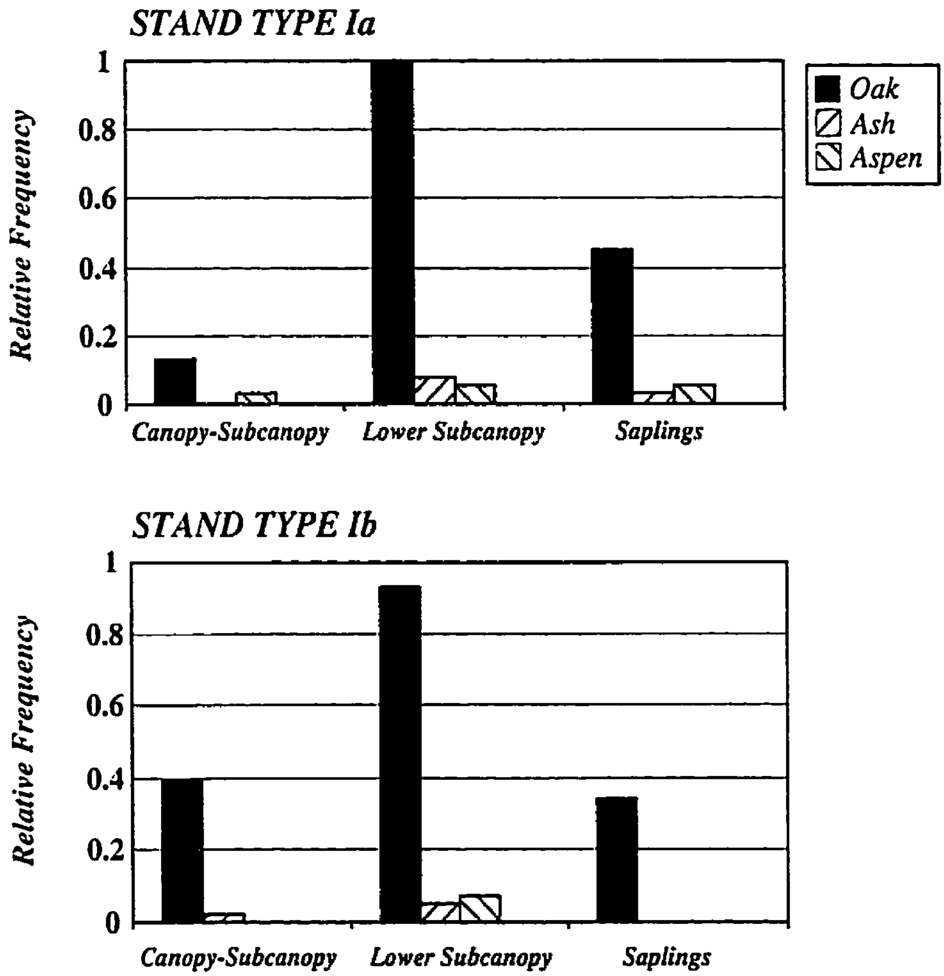


Fig. 5.4a. Relative frequency of tree species in the canopy-subcanopy (> 10 m height), lower subcanopy (2-10 m), and sapling (0.5 - 2 m) layers, stand type I.

1992). Fire suppression will increase fuel loads, resulting in much hotter fires that may kill some or most of the trees.

5.4.2 Stand Type II (Oak – Tall Shrub)

The successional trajectories for both sub-types have a strong directional component (**Fig. 5.3**). Sub-type IIa shows a shift in dominance from *Q. macrocarpa* in the canopy and subcanopy layers toward a mixture of *Q. macrocarpa* and *F. pennsylvanica* in the sapling layer (**Fig. 5.4b**). This suggests that *F. pennsylvanica* may become a more significant component of these stands over time, although *Q. macrocarpa* is also regenerating well and is expected to persist as a co-dominant. Sub-type IIb shows a shift from a mixture of *Q. macrocarpa*, *F. pennsylvanica* and *P. tremuloides* (occasionally *P. balsamifera*) in the canopy, to co-dominance of *Q. macrocarpa* and *F. pennsylvanica* in the lower subcanopy, and dominance of *F. pennsylvanica* in the sapling layer. This indicates that these stands will shift toward greater dominance of *F. pennsylvanica*, and to a lesser extent *Q. macrocarpa*, as the mature *P. tremuloides* trees die and fall out of the canopy. In these stands, regeneration of *Q. macrocarpa* is compromised by the dense canopy layer and strong interspecific competition for light from the dense shrub layer. Oak recruitment may increase following the creation of canopy gaps as the aspen die.

These stands will gradually shift toward greater *F. pennsylvanica* dominance in the absence of a catastrophic disturbance. Tall shrubs dominate the understory, forming a dense cover that casts a deep shade and limits *Q. macrocarpa* recruitment. Under such conditions, there is widespread potential for *Q. macrocarpa* to be replaced by more shade-tolerant species such as *F. pennsylvanica* (Christensen 1977, Lorimer 1984, McCune & Cottam 1985, Nowacki et al. 1990).

5.4.3 Stand Type III (Oak – Aspen – Ash)

The successional trajectories for both sub-types are strongly directional (**Fig. 5.3**). The trajectory for sub-type IIIa is similar to that of sub-type IIb, shifting from *Q. macrocarpa*–

P. tremuloides codominance in the canopy, to *Q. macrocarpa* - *F. pennsylvanica* codominance in the lower subcanopy, and dominance of *F. pennsylvanica* (with some recruitment of *Q. macrocarpa* and *A. negundo*) in the sapling layer (**Fig. 5.4c**). This suggests that *P. tremuloides* will become a minor component of these stands over time, with a shift in dominance toward shade-tolerant, later successional species such as *F. pennsylvanica* and *A. negundo* that are intolerant of fire. A similar but stronger trend is present in sub-type IIIb, shifting from a mixed forest of *Q. macrocarpa*, *F. pennsylvanica*, *P. tremuloides* and *A. negundo* in the canopy, to codominance of *F. pennsylvanica* and *A. negundo* in the lower subcanopy, and *F. pennsylvanica* and *A. negundo* in the sapling layer. This is the only sub-type in which *Q. macrocarpa* was not present in the sapling layer. This is likely attributable to the deeply shaded conditions (a combination of a dense canopy-subcanopy layer and high tall shrub cover) that characterize these stands. *Q. macrocarpa* relies on the opening of canopy gaps, and as a result is expected to persist as a minor component of these stands.

Fires occur infrequently in these stands, as evidenced by the presence of *F. pennsylvanica* and *A. negundo* (both of which are fire-intolerant). The mesic conditions of these are less conducive to frequent, high intensity fires, favoring shade-tolerant, late-successional tree species. Only a high intensity fire would be able to have significant effects on canopy mortality and replacement (Abrams 1985).

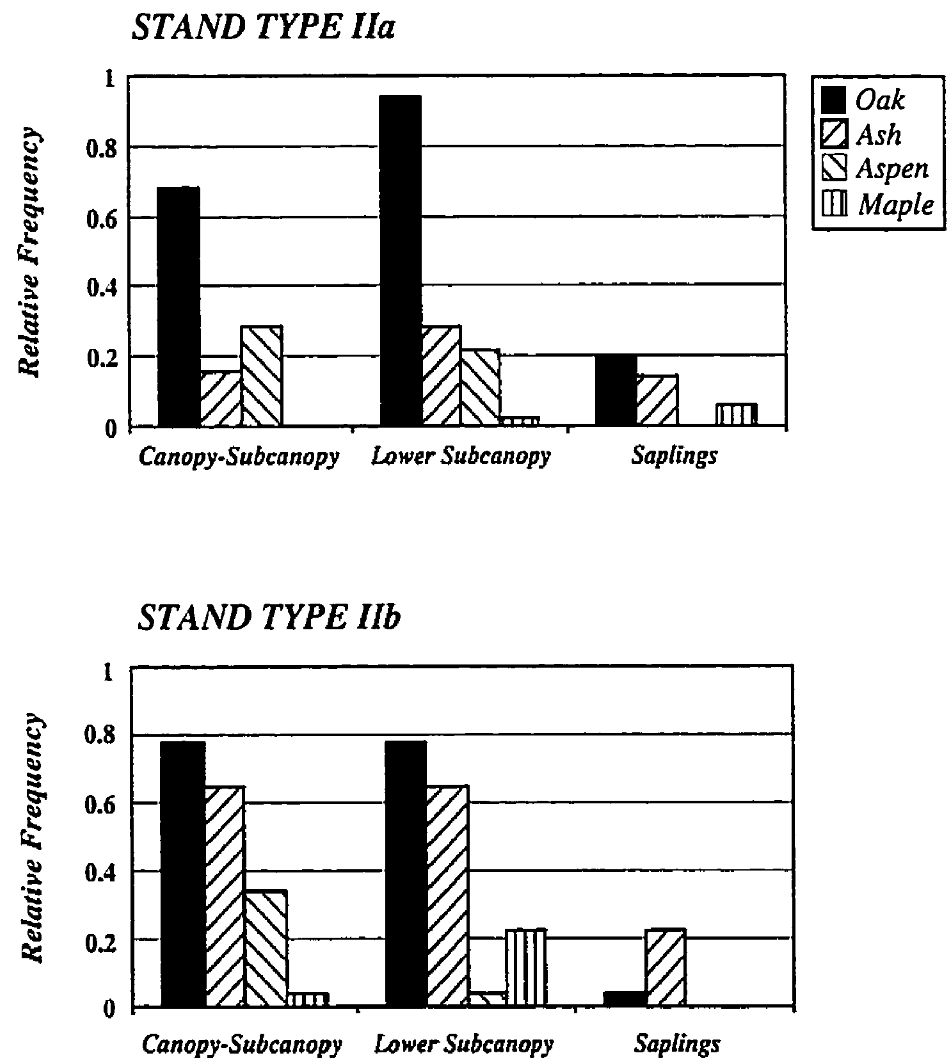
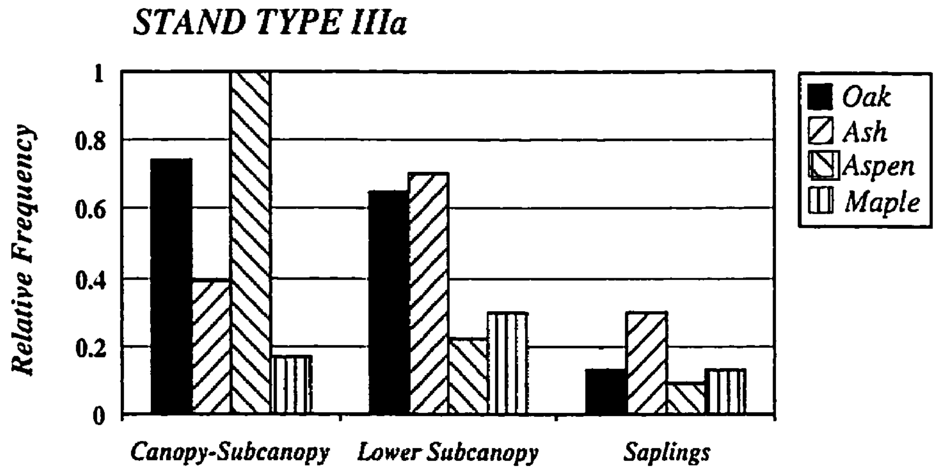


Fig. 5.4b. Relative frequency of tree species in the canopy-subcanopy (> 10 m height), lower subcanopy (2-10 m), and sapling (0.5 - 2 m) layers, stand type II.



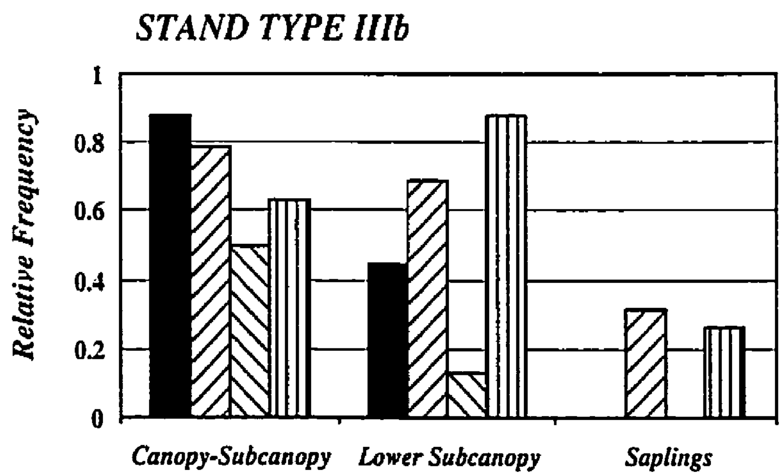


Fig. 5.4c. Relative frequency of tree species in the canopy-subcanopy (> 10 m height), lower subcanopy (2-10 m), and sapling (0.5 - 2 m) layers, stand type III.

CHAPTER 6
MANAGEMENT RECOMMENDATIONS

Both short and long term goals should be considered when establishing guidelines for management recommendations. Because *Quercus macrocarpa* is a long-lived species, any management considerations should take into account all possible long-term effects.

6.1 Establishment of Permanent Plots

Permanent plots should be established for long-term monitoring of population and community dynamics (Chapman 1993). Monitoring would be used to observe and quantify changes in species composition and abundance, including seedling establishment and growth of advanced regeneration, canopy tree growth rates, pest and pathogen outbreaks, soil characteristics and development, and ungulate herbivory and other evidence of disturbance (Brewer 1993).

6.2 Fire Management

Prescribed burning is the single most important management tool in the restoration and management of oak savanna ecosystems (Tester 1989, Leach 1995). In Riding Mountain National Park, past fire suppression has resulted in increased of fuel loads (mainly the result of tall shrub encroachment), which may increase the risk of stand-replacing fires to which *Q. macrocarpa*, *Fraxinus pennsylvanica*, *Acer negundo* and *Ulmus americana* are poorly adapted. Substantial shrub encroachment is particularly a problem in oak savannah stands along the northeastern border of the Park (e.g. Agassiz Ski Road). A dense shrub cover can result in hotter, more damaging fires. In addition, the shrub layer casts a deep shade that limits *Q. macrocarpa* regeneration and shades out the native understory vegetation, reducing biodiversity and compromising ecosystem sustainability. Carefully controlled prescribed burns in early spring may be effective in reducing understory fuel loads while also minimizing the severity and extent of the fire (McCarty 1993). Prescribed burning is not recommended on steep, south-facing slopes that are subject to erosion. In addition, prescribed burning should not be considered in mesic mixed-forest stands, since most of the tree species present in these stands are very intolerant of fire (e.g. *F. pennsylvanica, A. negundo, U. americana*). A fire in these stands would favor early-successional boreal species such as *P. tremuloides* and *P. balsamifera*, and would also be highly detrimental to the forest understory.

6.3 Mechanical Reduction of Fuel Loads

Mechanical fuel reduction (possibly including selective cutting) is often recommended prior to burning, particularly when fire suppression has been practiced in the past and fuel buildups are appreciable (as has occurred in Riding Mountain National Park). If fuel loads are not reduced prior to a prescribed burn, the fire will burn too hot resulting in considerable damage to trees and high tree and understory mortality. Mechanical brush removal is a commonly used method for restoring oak savanna in the United States, but it is expensive and very labor-intensive (Chapman 1993). Mechanical reduction serves three purposes: (a) it allows light to penetrate to the ground, favoring the herb layer; (b) it reduces the fuel load, reducing the chance of a stand-replacing fire; and (c) it mimics the effects of a low intensity burn, and promotes oak regeneration (McCarty 1993). Mechanical fuel reduction may be useful in stand-type II to reduce shrub density and cover. If fuel loads were not first reduced, a prescribed burn in these sites would likely be catastrophic. Degraded *Q. macrocarpa* stands have been restored by first reopening the understory to increase light penetration, followed by reinstatement of the historic fire regime (Leach 1993). A detailed description of this and similar strategies for *Q. macrocarpa* savanna management is presented in Chapter 1.

6.4 Grazing

Intense ungulate browsing of *Q. macrocarpa* was observed in clearing and openings of stand-type I. Occasionally, severe damage was observed in the regenerating layer in these xeric sites. The effect of ungulate browsing on these long-lived, slow-growing trees should be carefully monitored to ensure that their long-term integrity is not compromised.

6.5 Mitigation of Human Disturbances

Many *Q. macrocarpa* stands are found along roadways and trails in the Park. Most back-country trails are not extensively used by the public (e.g. Payne, Thacker, North Escarpment Trails), and little human disturbance was observed. More accessible trails (e.g. Gorge Creek and Packhorse Trails) are used often by both hikers and cyclists. Many oak trees in these sites are very old for their size (over 300 years, but only 2 m tall), and they are highly vulnerable to disturbance or vandalism. The public should be educated as to the ecological importance and sensitivity of these stands.

6.6 Future Research

Future research on these *Quercus* stands should be done for further understanding and better management in the future. Impact of herbivory on xeric sites should be studied as these stands were heavily browsed and therefore susceptible to degradation. A study of the fauna which rely on the *Quercus* stands would also provide information on current impacts on these stands. A detailed fire history study on these and structurally similar stands would provide much needed information to better understand the natural fire cycle. This research would allow managers to make informed decisions on management guidelines for the *Quercus* stands in Riding Mountain National Park.

CHAPTER 7

SUMMARY

(1) *Quercus macrocarpa* is a long-lived, wide-ranging species that nears its northwestern distributional limit in Riding Mountain National Park. Monodominant *Q. macrocarpa* stands were located on xeric sites, such as old beach ridges, steep slopes and outwash plains. *Q. macrocarpa* was also found mixed with other tree species in more mesic sites. In this study, 191 sample plots were enumerated to assess the environment, structure, composition, age structure, and regeneration dynamics of *Q. macrocarpa* stands.

(2) Cluster analysis was used to delineate the sample plots into three stand types, each with two subtype variants: I. = Oak – Low Shrub, Ia = very xeric (n = 38), Ib = xeric (n = 41); II. = Oak – Tall Shrub, IIa = subxeric (n = 50), IIb = submesic (n = 23); III. = Oak – Aspen – Ash, IIIa = subhygric (n = 23), IIIb = hygric (n = 16).

(3) The correspondence analysis ordination of the 191 plots and species shows a clear separation of the three stand types along the first ordination axis. Based on the distribution of the vegetation along this axis it is interpreted as a soil-moisture gradient. The most xeric sites occur on the left side of the ordination while mesic sites are on the far right. Species characteristic of xeric conditions include species such as *Crataegus chrysocarpa*, *Arctostaphylos uva-ursi*, *Viburnum rafinesquianum*, and *Schizachne purpurascens*. Rich woodland species characteristic of moist, shaded conditions include *Acer spicatum*, *Viburnum trilobum*, *Matteuccia struthopteris*, *Pyrola asarifolia*, and *Mitella nuda*. Species that occur in the center of the ordination, such as *Q. macrocarpa* and *Fragaria virginiana*, are either generalists or species that prefer intermediate moisture conditions.

(4) The second axis of the correspondence analysis is less well defined, only separating the two subtypes of stand type III. It is interpreted as a nutrient gradient with

nutrients increasing from bottom to top. *M. struthopteris* which is characteristic of moist, high nutrient sites occurs at the top, right of the ordination. *Equisetum pratense* and *Petasites sagittatus*, which are species characteristic of moist, low nutrient sites, occur at the bottom, right of the ordination.

(5) Canonical correspondence analysis also showed similar results as the correspondence analysis ordination, indicating the underlying soil moisture gradient is very strong. This ordination also confirms that species assemblages in the *Q. macrocarpa* stands are closely associated with environmental conditions. Xeric sites of stand type I are commonly found on steep, south-facing slopes and on gravelly outwash plains of the Manitoba Escarpment. The substrates are coarse, well-drained, with a thin organic layer and low nutrient status. Stand type II is commonly found on moderately drained old beach ridges, and flat benches of the Manitoba Escarpment. The nutrient status is low to moderate. The mesic sites of Stand type III are found at lower elevations at the base of the Manitoba Escarpment. The substrates characteristically have a greater soil organic matter accumulation, higher pH, higher conductivity and soils with a high clay content.

(6) Species richness is highly correlated with environmental conditions. Tree species richness is approximately 1 in stand type I, indicating that these are monodominant *Q. macrocarpa* stands. However, the understory is diverse with an effective species richness of 10. The conditions in these xeric sites are too harsh for other tree species, while the high light environment allows many grassland species to colonize. Stand type II has a tree species richness of 2 and an understory richness of 8. This stand type has intermediate species richness between the xeric and mesic stand types. Stand type III has the most diverse canopy with a tree species richness of 4, while understory richness is the lowest with a value of 5. More tree species are able to colonize these mesic sites creating mixed stands. However, increased tall shrub and tree cover shades the understory which limits species richness.

(7) *Q. macrocarpa* dominates all layers of the canopy in stand type I. Trees in this stand type have a short, shrubby growth due to the xeric growing conditions. *Fraxinus pennsylvanica* and *Populus tremuloides* and *Picea glauca* rarely occur in these stands. *V. rafinesquianum* and *Amelanchier alnifolia* dominate the shrub layer. *Corylus cornuta*, *C. chrysocarpa* and *Prunus virginiana* also occur frequently but at a lower cover value. Low shrubs such as *Rhus radicans*, *Rosa acicularis*, and *Symphoricarpos occidentalis* commonly occur. *A. uva-ursi*, a rare species in the Park, occurs occasionally on xeric, steep sites. Herbaceous diversity is high in this stand type due to the high light conditions. Sedges *Carex peckii* and *C. pensylvanica* are present in every site, while grass species, *Oryzopsis asperifolia*, *S. purpurascens*, and *Poa pratensis* are also commonly present. Characteristic forb species include *Monarda fistula*, *Lysimachia ciliata*, *Achillea millefolium*, *F. virginiana*, and *Aster ciliolatus*.

(8) *Q. macrocarpa* dominates all layers of the canopy in stand type II, except in the upper canopy of subtype IIb where very tall individuals of *P. tremuloides* or *Populus balsamifera* may occur. *F. pennsylvanica* and *P. tremuloides* also occur in the subcanopy. *C. cornuta* and *A. alnifolia* dominate the shrub layer while *P. virginiana*, *Cornus stolonifera*, *V. rafinesquianum*, *R. radicans*, and *R. acicularis* are also common at lower cover values. The herb layer is almost completely dominated by wild *Aralia nudacaulis*. Other herbs commonly encountered at lower cover values include *Sanicula marilandica*, *Maianthemum canadense*, *Solidago canadensis*, and *O. asperifolia*.

(9) In stand type III, *P. tremuloides* dominates the upper canopy while *Q. macrocarpa*, *A. negund)* and *F. pennsylvanica* dominate the subcanopy. *C. cornuta* dominates the understory. Other tall shrubs such as *A. spicatum*, *V. trilobum*, *Viburnum lentago* and *A. alnifolia* are also present at lower cover values. Low shrubs are uncommon. Herbaceous diversity is high, however herb cover values are low. Other characteristic

species of these mesic sites include *A. nudacaulis*, *M. struthopteris*, *P. sagittatus*, *M. nuda*, *Trillium cernuum* and *Anemone quinquefolia*.

(10) The growth rates of *Q. macrocarpa* vary in all stand types. Trees growing in the most xeric sites had the slowest growth rate while trees in the mesic sites had the greatest growth. These results suggest that *Q. macrocarpa* growth is limited by moisture availability. As the amount of available moisture increases, the diameter of the tree increases accordingly. Xeric sites have little moisture, therefore the increase in the diameter of the trees is very small. Trees in mesic sites with increased moisture availability have a greater increase in the diameter.

(11) Since *Q. macrocarpa* is shade intolerant, regeneration is limited in closed forest stands and in sites with high shrub cover. This suggests that light, rather than soil moisture is the greatest factor contributing to *Q. macrocarpa* recruitment in RMNP. *Q. macrocarpa* regeneration in stand type I is high, as an average of 17 seedlings and sucker shoots per plot were encountered. These stands have open canopies and high light conditions promoting regeneration. Regeneration in stand type II is low to moderate. Increased shrub cover creates lower light conditions in these sites limiting the amount of *Q. macrocarpa* recruitment. Stand type III has low recruitment of *Q. macrocarpa*. These sites have a dense, closed canopy and a high cover of tall shrubs, which shade out *Q. macrocarpa* seedlings.

(12) Using size-class ordination analysis, possible future stand structures for the three stand types were summarized. The successional vectors indicate that the canopy and subcanopy of both subtypes in stand type I are undergoing little change. Regeneration of *Q. macrocarpa* is high in these sites as the conditions are too extreme for other tree and shrub species. Therefore, both subtypes are self-replacing. The successional vectors for both subtypes in stand type II are strongly directional. Subtype IIa shows a shift in dominance from *Q. macrocarpa* to a mixture of *Q. macrocarpa* and *F. pennsylvanica*. Subtype IIb shows a shift in

dominance from a mixture of *Q. macrocarpa, F. pennsylvanica* and *P. tremuloides* to co-dominance of *Q. macrocarpa* and *F. pennsylvanica* in the subcanopy and dominance of *F. pennsylvanica* in the sapling layer. Therefore, these stands will gradually shift toward greater *F. pennsylvanica* dominance. The successional vectors for both subtypes in stand type III are also strongly directional. Subtype IIIa shows a shift from *Q. macrocarpa-P. tremuloides* codominance to *Q. macrocarpa-F. pennsylvanica* in the lower subcanopy, and dominance of *F. pennsylvanica* in the sapling layer. Subtype IIIb shows a stronger trend towards codominance of *F. pennsylvanica* and *A. negundo* from a mixed stand of *Q. macrocarpa, F. pennsylvanica, P. tremuloides* and *A. negundo. Q. macrocarpa* is expected to persist only as a minor component of these stands.

(13) Management guidelines were suggested to maintain *Q. macrocarpa* stands in Riding Mountain National Park. Establishment of permanent plots should be set up to monitor long-term effects in all stand types. Prescribed burning is recommended for stand type II, but not for stand types I and III. Mechanical reduction of the fuel load in the understory is recommended for stand type II prior to prescribed burning. This will decrease the intensity of the fire, reducing the potential for *Q. macrocarpa* trees to be killed. Ungulate browsing should be monitored over the long term to ensure long-term integrity is not compromised. Human disturbance along backcountry trails should also be monitored and the public should be informed as to the ecological importance and sensitivity of the stands. Future research is needed on fire history and fauna populations to provide managers to make informed decisions on management guidelines.

REFERENCES

Abrams, M. D. 1984. Fire history of oak gallery forests in a northeast Kansas tallgrass prairie. Am. Midl. Nat. 114(1):188-191.

Abrams, M. D. 1986. Historical development of gallery forests in northeast Kansas. Vegetatio 65:29-37.

Abrams, M. D. 1992. Fire and the development of oak forests. BioScience 42:346-353.

Abrams, M. D. & A. K. Knapp. 1986. Seasonal water relations of three gallery forest hardwood species in northeast Kansas. For. Sci. 32:687-696.

Ahlgren, C. E. 1957. Phenological observations of nineteen native tree species in northeastern Minnesota. Ecology. 38(4):622-628.

Allen, M., Kuta, G. 1994. Oak decline. Nat. Resour. Can., Can. For. Serv., Northwest Reg., North. For. Cent., Edmonton, Alberta. For. Leafl. 28.

Alverson, W.S., W. Kuhlmann, and D.M. Waller. 1994. Wild Forests: Conservation Biology and Public Policy. Island Press, Washington, D.C. 300 pp.

Anderson, R. C. & L.E. Brown. 1983. Comparative effects of fire on trees in a midwestern savannah and an adjacent forest. Bull. Torrey. Bot. Club. 110 (1):87-90.

Andersson, C. 1991. Distribution of seedlings and saplings of *Quercus robor* in a grazed deciduous forest. J. Veg. Sci. 2:279-282.

Batzer, H.O. and R. Morris. 1978. Forest Tent Caterpillar. Forest Insect and Disease Leaflet 9. USDA Forest Service.

Bey, C.F. 1990. *Ulmus americana*. Pages 801-807 in Burns, R.M & B.H. Honkala (eds.) 1990. Silvics of North America:2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Bird, R.D. 1961. Ecology of the Aspen Parkland. Agriculture Canada. Winnipeg, Manitoba.

Bragg, T. B. & L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Manag. 29:19-24.

Braun, E. L. 1950. Deciduous Forest of Eastern North America. The Blakiston Company, Toronto, Ontario.

Bray, J. R. 1958. The distribution of savanna species in relation to light intensity. Can. J. Bot. 36:671-681.

Bray, J. R. 1960. The composition of savanna vegetation in Wisconsin. Ecology 41:721-723.

Buell, M. F. & J. E. Cantlon. 1951. A study of two forest stands in Minnesota with an interpretation of the prairie-forest margin. Ecology 32:294-316.

Carvell, K. L. & E. H. Tryon. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. For. Sci. 7(2):98-105.

Chapman, K. A., M. A. White, M. R. Huffman & D. Faber-Langendoen. 1993. Ecology and stewardship guidelines for oak barrens landscapes in the upper midwest in Proceedings of the 1993 Midwest Oak Savanna Conference. www.epa.gov/glnpo/oak/oak93

Christensen, N.L. 1977. Changes in structure, pattern, and diversity associated with climax forest maturation in Piedmont, North Carolina. Am. Midl. Nat 97:176-188.

Cody, W.J. 1988. Plants of Riding Mountain National Park, Manitoba. Agriculture Canada. Ottawa.

Collins, S. L. & S. C. Klahr. 1991. Tree dispersion in oak-dominated forests along an environmental gradient. Oecologia 86:471-477.

Corkery, M.T. Geology and Landforms of Manitoba in Welsted, J., J. Everitt & C. Stadel (eds.). 1996. The Geography of Manitoba:Its Land and Its People. The University of Manitoba Press. Winnipeg, Manitoba.

Cottam, G. 1949. The phytosociology of an oak woods in southwestern Wisconsin. Ecology 30:271-287.

Cronquist, A. 1988. The Evolution and Classification of Flowering Plants. The New York Botanical Garden. New York. 555 pp.

Crow, T. R. 1988. Reproductive mode and mechanisms for self-replacement of Northern Red Oak (*Quercus rubra*) - a review. For. Sci. 34:19-40.

Crum, H.A. 1976. Mosses of the Great Lakes forest. Rev. ed. Contributions from the Universisty of Michigan Herbarium, vol.10. Ann Arbor. 404 pages.

Curtis, J. T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison.

Darley-Hill, S. and W.C Johnson. 1981. Acorn dispersal by the blue jay. Oecologia 50:231-232.

Daubenmire, R. F. 1936. The "big woods" of Minnesota:its structure, and relation to climate, fire, and soils. Eco. Mono. 6(2):233-268.

Davis, M. A., K. J. Wrage & P. B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation:support for a theory of resource supply and demand. J. Ecology 86:652-661.

Day, G.M. 1953. The Indian as an ecological factor in the northeastern forest. Ecology 34:329-346.

Delcourt, P. A. & H. R. Delcourt. 1985. Long-Term Forest Dynamics of the Temperate Zone. Springer-Verlag. New York.

Dooley, K. L. & S. L. Collins. 1984. Ordination and classification of western oak forests in Oklahoma. Amer. J. Bot. 71(9):1221-1227.

Dorney, C.H. & J.R. Dorney. 1989. An unusual oak savanna in northwestern Wisconsin (USA). The effect of Indian-caused fire. Am. Midl. Nat. 122 (1):103-113.

Dougherty, P. M. & T. M. Hinckley. 1981. The influence of a severe drought on net photosynthesis of white oak (*Quercus alba*). Can. J. Bot. 59:335-341.

Dreistadt, S.H. 1994. Pests of Landscape Trees and Shrubs:An Integrated Pest Management Guide. Oakland, CA. 327pp.

Dunbar, D.M. and G. Stephens. 1975. Association of twolined chestnut borer and shoestring fungus with mortality of defoliated oak in Conneticut. For. Sci. 21 (2):169-174.

Dunn, J.P., T. Kimmerer, and G. Nordin. 1986. Attraction of the twolined chestnut borer, *Agrilus Bilineatus* (Weber) (Coleoptera:Buprestidae), and associated borers t volatiles of stressed white oak. Can. Ent. 118:503-509.

Dyksterhuis, E.J. 1957. The savannah concept and its use. Ecology 38:435-442.

Faber-Langendoen, D. (ed.). 1995. The Nature conservancy's Natural community classification and its application to midwest oak savannas and woodlands in 1995 Midwest Oak Savanna and Woodland Ecosystems Conference. www.epa.gov/glnpo/oak/oak95

Farrar, J. L. 1995. Trees in Canada. Fitzhenry & Whiteside Limited. Markham, Ontario.

Fuller, L .G. & D. W. Anderson. 1993. Changes in soil properties following forest invasion of Black soils of Aspen Parkland. Can. J. Soil. 73:613-627.

Geobel, P. C. & D. M. Hix. 1996. Development of mixed-oak forests in southeastern Ohio:a comparison of second-growth and old-growth forests. For. Ecol. Manage. 84:1-21.

Goodrum, P. D., V. Reid & C. Boyd. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. J. Wild. Manage. 35:520-531.

Grimm, E.C. 1984. Fire and other factors controlling the big woods vegetation of Minnesota in the mid-nineteenth century. Eco. Mono. 53:291-311.

Haack, R.A. and R.E. Acciavatti. 1992. Twolined chestnut borer. U.S. Dep. Agric. For. Serv. Forest Insect and Disease Leaflet 168.

Haack, R.A. and M. Benjamin. 1982. The biology and ecology of the twolined chestnut borer, *Agrilus bilineatus* (Coleoptera:Buprestidae), on oaks, *Quercus* spp. in Wisconsin. Can. Ent. 114:385-396.

Hamerlynck, E .P. & A. Knapp. 1994. Leaf-level responses to light and temperature in two co-occurring *Quercus* (Fagaceae) species:implications for tree distribution patterns. For. Ecol. Manage. 68:149-159.

Haney, A. & S. I. Apfelbaum. 1993. Characterization of midwestern oak savannas in 1993 Midwest Oak Savanna and Woodland Ecosystems Conference. www.epa.gov/glnpo/oak/oak93

Hengst, G. E. & J. O. Dawson. 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. Can. J. For. Res. 24:688-696.

Hiratsuka, Y. 1987. Forest Tree Diseases of the Prairie Provinces. Northern Forestry Service. Edmonton, Alberta. 142pp.

Holechek, J.L., M. Vavra, J. Skovlin, and W. Kruger. 1982. Cattle diets in the Blue Mountains of Oregon Forests. J. Range Manage. 35:239-242.

Holloway, R. G. & V. M. Bryant. 1985. Late-quaternary pollen records and vegetational history of the Great Lakes region:United States and Canada. Pages 205-240 in Bryant, V. M. & R. G. Holloway (eds.). 1985. Pollen records of late-Quaternary North American sediments. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas.

Hosner, J. F. & L. S. Minckler. 1963. Bottomland hardwood forests of southern Illinois - regeneration and succession. Ecology 44:29-41.

Host, G. E., K. S. Pregitzer, C. W. Ramm, J. B. Hart, & D. T. Cleland. 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern Lower Michigan. For. Sci. 33:45-457.

Howell, D.L. & C.L. Kucera. 1956. Composition of presettlement forests in three counties in Missouri. Bull. Tor. Bot. Club 83:297-217.

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69:46-58.

Ives, W.G.H., and Wong, H.R. 1988. tree and shrub insects of the prairie provinces. Can. For. Serv., North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-292.

Johnson, V. J. 1984. Prescribed burning - requiem or renaissance? J. For. 32:82-91.

Johnson, P. S. 1990. *Quercus macrocarpa*. Pages 682-692 in Burns, R. M. & B. H. Honkala (eds.). 1990. Silvics of North America: 2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Johnson, W. C., R. L. Burgess & W. R. Keammerer. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. Ecol. Mono. 46:59-84.

Johnson, V.J. & W.A. Main. 1978. A climatology of prescribed burning. Proceedings of the Fifth Joint conference on Fire and forest Meterology. New Jersey.

Keammerer, W. R., W. C. Johnson & R. L. Burgess. 1975. Floristic analysis of the Missouri River bottomland forests in North Dakota. Can. Field. Nat. 89(1):5-19.

Kennedy, H.E. 1990. *Fraxinus pennsylvanica*. Pages 348-354 in Burns, R.M & B.H. Honkala (eds.) 1990. Silvics of North America:2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Killingbeck, K. T. & M. K. Wali. 1978. Analysis of a North Dakota gallery forest:nutrient, trace element and productivity relations. OIKOS 30:29-60.

Killingbeck, K. T. & R. Bares. 1978. Vegetation and soils of a gallery forest bordering Homme Reservoir, North Dakota. Annual Proceedings of the North Dakota Academy of Science 31:40-49.

Klassen, R. W. 1989. Quaternary geology of the southern Canadian Interior Plains. Pages 138-173 in Fulton, R. J. (ed.). 1989. Quaternary geology of Canada and Greenland. Geological Survey of Canada, Geology of Canada, No. 1.

Kline, V. M. & C. Cottam. 1979. Vegetation response to climate and fire in the driftless area of Wisconsin. Ecology 60(5):861-868.

Knapp, K.C. 1992. Leaf exchange in *Quercus macrocarpa*:rapid stomatal responses to variability in sunlight in a tree growth form. Am. J. Bot. 79:599-604.

Kneeshaw, D. D. & Y. Bergeron. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79(3):783-794.

Laing, C. L. 1966. Bur oak seed size and shadiness of habitat in southeastern Nebraska. Am. Midl. Nat. 76(2):534-536.

Leach, M. K. & L. Ross. 1995 (eds.). Midwest oak ecosystems recovery plan:A call to action. in 1995 Midwest Oak Savanna and Woodland Ecosystems Conference. www.epa.gov/glnpo/oak/oak95

LeBlanc, D. C. 1998. Interactive effects of acidic deposition, drought, and insect attack on oak populations in the midwestern United States. Can. J. For. Res. 28:1184-1197.

Lorimer, C. G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. Ecology 58:139-148.

Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. For. Sci. 30:3-22.

Lorimer, C. G., J. W. Chapman & W. D. Lambert. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. 82:227-237.

McCarty, K. 1993. Restoration in Missouri savannas. Proceedings of the Oak Savanna Conference, February 20, 1993, Northeastern Illinois University, Chicago.

McCarty, K. 1995. Restoration in Missouri savannas. Proceedings of the Oak Savanna Conference. Northeastern Illinois University, Chicago.

McClain, W. E., M. Jenkins, S. Jenkins & J. Ebinger. 1993. Changes in the woody vegetation of a bur oak savanna remnant in central Illinois. Nat. Area. J. 13(2):109-114.

McCune, B. & G. Cottam. 1985. The successional status of a southern Wisconsin oak woods. Ecology 66(4):1270-1278.

McManus, M., N. Schneeberger, R. Reardon, and G. Mason. 1987. Gypsy Moth. Forest Insect and Disease Leaflet 162. UDSA Forest Service.

McQuilkin, R. A. 1990. *Quercus palustris* Muenchh. Pages 709-714 in Burns, R.M. & B. H. Honkala (eds.). 1990. Silvics of North America: 2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Monette, R., & S. Ware. 1983. Early forest succession in the Virginia Coastal Plain. Bull. Torrey Bot. Club 110:80-86.

Mlot, C. 1990. Restoring the prairie. Bioscience 40(11):804-809.

Nowacki, G.J., M.D. Abrams, and C.G. Lorimer. 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. For. Sci. 36:276-292.

Old, S. 1969. Microclimate, fire and plant production in an Illinois prairie. Eco. Mono.. 39:355-384.

Overton, R.P. 1990. *Acer negundo*. Pages 41-45 in Burns, R.M & B.H. Honkala (eds.) 1990. Silvics of North America:2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Packard, S. and J. Balaban. 1994. Restoring the herb layer in a degraded bur oak "closed" savanna. In, J.S. Fralish, R.C. Anderson, J.E. Ebinger, and R. Szafoni (eds.), Proceedings of the North American Conference on Barrens and Savannas. U.S. Environmental Protection Agency, Great Lakes National Program Office, Chicago, Illinois. Pp. 247-251.

Peet, M., R. Anderson, and M. Adams. 1975. Effect of fire on big bluestem production. Am. Midl. Nat 94:15-26.

Perala, D.A. 1990. *Populus tremuloides*. Pages 555-569 in Burns, R.M & B.H. Honkala (eds.) 1990. Silvics of North America:2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Podani, J. 1994. Multivariate Data Analysis in Ecology and Systematics:A methodological guide to the Syntax 5.0 package. Acadenic Publ. The Hague, The Netherlands.

Reich, P. B., R. O. Teskey, P. S. Johnson & T. M. Hinckley. 1980. Periodic root and shoot growth in oak. For. Sci. 26(4):590-598.

Reich, P.B., M.D. Abrams, D.S. Ellsworth, E.L. Kruger, and T.J. Tabone. 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71(6):2179-2190.

Reily, P. W. & W. C. Johnson. 1982. The effects of altered hydrologic regime on tree growth along the Missouri River in North Dakota. Can. J. Bot. 60:2410-2423.

Rexrode, C.O. and D. Brown. 1983. Oak Wilt. Forest Insect and Disease Leaflet. UDSA Forest Service.

Rice, E. L. & W. T. Penfound. 1959. The upland forests of Oklahoma. Ecology 40(4):593-608.

Rice, E.L., and R.L. Parenti. 1978. Causes of decreases in productivity in undisturbed tall grass prairie. Amer. J. Bot. 65:1091-1097.

Riding Mountain National Park. 1993. Riding Mountain National Park Trail Guide. Leech Printing Ltd. Brandon, Manitoba.

Riding Mountain National Park. 1998. Riding Mountain National Park Web Page.

Ritchie, J. C. 1964. Contributions to the holocene paleoecology of westcentral Canada. I. The Riding Mountain area. Can. J. Bot. 42:181-193.

Ritchie, J. C. 1985. Quaternary pollen records from the Western Interior and the Arctic of Canada. Pages 327-352 in Bryant, V. M. & R. G. Holloway (eds.). 1985. Pollen records of late-Quaternary North American sediments. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas.

Ritchie, J. C. 1987. Postglacial Vegetation of Canada. Cambridge University Press, New York. 178 pp.

Ritchie, M. E., D. Tilman & J. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79(1):165-177.

Roath, L.R. and W. Krueger. 1982. Cattle grazing influence of a mountain riparian zone. J. Range. Manage. 35:100-103.

Rogers, R. 1990. *Quercus alba* L. Pages 605-613 in Burns, R. M. & B. H. Honkala (eds.). 1990. Silvics of North America: 2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Rowe, J.S. 1972. Forest regions of Canada. Dept.Envt., Can. For. Ser., Ottawa, Publ. No. 1300. 72 pages.

Sander, I. L. 1990. *Quercus rubra* L. Pages 727-733 in Burns, R.M. & B. H. Honkala (eds.). 1990. Silvics of North America: 2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Sauer, C. O., 1950. Grassland climax, fire, and man. J. Range Manag. 3:16-21.

Scott, G. A. 1996. Manitoba's Ecoclimatic Regions. Pages 43-55 in Welsted, J., J. Everitt & C. Stadel (eds.). 1996. The Geography of Manitoba: Its Land and Its People. The University of Manitoba Press. Winnipeg, Manitoba.

Severson, K. E. & J. J. Kranz. 1978. Management of bur oak on deer winter range. Wild. Soc. Bull. 6(4):212-215.

Sharp, W. J & V. G. Sprague. 1967. Flowering and fruiting in the white oaks. Pistillate flowering, acorn development, weather, and yields. Ecology 48:243-251.

Sieg, C. H. & H. A. Wright. 1996. The role of prescribed burning in regenerating *Quercus macrocarpa* and associated woody plant in Stringer Woodlands in the Black Hills, South Dakota. Int. J. Wildland Fire 6:21-29.

Soule, M. E. 1991. Conservation:Tactics for a constant crisis. Science 253:744-757.

Stephenson, S. L. 1986. Changes in a former chestnut dominated forest after a half century of succession. Am. Midl. Nat. 116:173-179.

Stransky, J. J. 1990. *Quercus stellata* Wangenh. Pages 738-743 in Burns, R.M. & B. H. Honkala (eds.). 1990. Silvics of North America: 2. Hardwoods. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1.

Szeicz, J. M. & G. M. MacDonald. 1991. Postglacial vegetation history of oak savanna in southern Ontario. Can. J. Bot. 69:1507-1519.

Tester, J. R. 1989. Effects of fire frequency on oak savanna in east-central Minnesota. Bull. Torrey. Bot. Club 116(2):134-144.

The Concise Oxford Dictionary (9th ed.). 1995. Clarendon Press. Oxford.

Uresk, D. W. & W. W. Painter. 1985. Cattle diets in a ponderosa pine forest in the northern Black Hills. J. Range. Manage. 38(5):440-442.

Van Dersal, W.R. 1940. Utilization of oaks by birds and mammals. J. Wild. Manage. 4:404-428.

Vitt, D.H., J.E. Marsh & R.B. Bovey. 1988. Mosses, lichens, and ferns of northwestern North America. Lone Pine Publishing, Edmonton, Alberta. 296 pages.

Wargo, P.M. 1977. *Armillariella mellea* and *Agrilus bilineatus* and mortality of defoliated oak trees. For. Sci. 23(4):485-492.

Wargo, P.M., D. Houston, and L. LaMadeleine. 1983. Oak Decline. Forest Insect and Disease Leaflet 165. USDA Forest Service.

Watts, W. A. 1980. Late Quaternary vegetation of the central Appalachian and the New Jersey coastal plain. Ecol. Monogr. 49:427-469.

Welsted, J., J. Everitt, and C. Stadel. 1996. Manitoba:Geographical Identity of a Prairie Province in Welsted, J., J. Everitt & C. Stadel (eds.). 1996. The Geography of Manitoba:Its Land and Its People. The University of Manitoba Press. Winnipeg, Manitoba.

Weaver, J. E. 1960. Flood plain vegetation of the central Missouri Valley and contacts of woodlands with prairie. Eco. Mono. 30:37-64.

Weaver, J.E. 1960. Prairie plants and their environment. Univ. of Nebraska Press, Lincoln. 276.

Weaver, J.E. & F.E. Clements. 1938. Plant Ecology. McGraw-Hill Book Co., New York. 601 pages.

Weaver, J. E. & J. Kramer. 1932. Root system of *Quercus macrocarpa* in relation to the invasion of prairie. Bot. Gaz. 94:51-85.

White, A. S. 1983. The effects of thirteen years of annual prescribed burning on a *Quercus ellipsoidalis* community in Minnesota. Ecology 64(5):1081-1085.

Whitford, P. B. & K. Whitford. 1971. Savanna in central Wisconsin. Vegetatio 23:77-87.

Whitford, P. B. & K. Whitford. 1978. Effects of trees on ground cover in old-field succession. Am. Midl. Nat. 99:435-443.

Wikum, D. A. & M. K. Wali. 1974. Analysis of a North Dakota gallery forest:vegetation in relation to topographic and soil gradients. Eco. Mono. 44:441-464.

APPENDIX 1

List Of Plant Species Encountered In Riding Mountain National Park

Appendix 1.Species list of the 191 Bur Oak sites enumerated during the 1998-1999 field seasons

Plant Form	Genus	Species	Common Name
Trees	*Abies*	*balsamea*	Balsam fir
	Acer	*negundo*	Manitoba maple
	Picea	*glauca*	White spruce
	Betula	*papyrifera*	Paper birch
	Fraxinus	*pennsylvanica*	Green ash
	Populus	*balsamifera*	Balsam poplar
	Populus	*tremuloides*	Trembling aspen
	Quercus	*macrocarpa*	Bur oak
	Ulmus	*americana*	American elm
Shrubs	*Acer*	*spicatum*	Mountain maple
	Amelanchier	*alnifolia*	Saskatoonberry
	Cornus	*stolonifera*	Red-osier dogwood
	Corylus	*cornuta*	Beaked hazelnut
	Crataegus	*chrysocarpa*	Hawthorn
	Prunus	*americana*	Wild plum
	Prunus	*pensylvanica*	Pin cherry
	Prunus	*virginiana*	Chokecherry
	Viburnum	*lentago*	Nannyberry
	Viburnum	*rafinesquianum*	Downy arrowwood
	Viburnum	*trilobum*	High bush-cranberry
	Arctostaphylos	*uva-ursi*	Bearberry
	Celastrus	*scandens*	Bittersweet
	Diervilla	*lonicera*	Bush-honeysuckle
	Lonicera	*dioica*	Twining honeysuckle
	Potentilla	*species*	Cinquefoil
	Rhus	*radicans*	Poison ivy
	Parthenocissus	*inserta*	Virginia creeper
	Ribes	*glandulosum*	Skunk currant
	Ribes	*hudsonianum*	Northern black currant
	Ribes	*oxycanthoides*	Northern gooseberry
	Ribes	*triste*	Red currant
	Rosa	*acicularis*	Prickly rose
	Rubus	*idaeus*	Raspberry
	Salix	*species*	Willow species
	Shepherdia	*canadensis*	Buffaloberry
	Symphoricarpos	*albus*	Snowberry
	Symphoricarpos	*occidentalis*	Wolfberry

Plant Form	Genus	Species	Common Name
Herbs	*Achillea*	*millefolium*	Common yarrow
	Actaea	*rubra*	Red baneberry
	Agastache	*foeniculum*	Giant-hyssop
	Amphicarpa	*bracteata*	Hog-peanut
	Anemone	*canadensis*	Canada anemone
	Anenome	*quinquefolia*	Wood anemone
	Apocynum	*androsaemifolium*	Spreading dogbane
	Aquilegia	*canadensis*	Wild columbine
	Aralia	*nudacaulis*	Wild sarsaparilla
	Arenaria	*lateriflora*	Grove sandwort
	Arctium	*minum*	Burdock
	Aster	*ciliolatus*	Fringed aster
	Bromus	*ciliolatus*	Fringed brome
	Bromus	*inermis*	Northern brome
	Caltha	*palustris*	Marsh-marigold
	Campanula	*rotundifolia*	Bluebell
	Carex	*peckii*	Sedge species
	Carex	*pedunculata*	Sedge species
	Carex	*pensylvanica*	Sedge species
	Cicuta	*maculata*	Water-hemlock
	Comandra	*umbellata*	Bastard toadflax
	Convolvulus	*sepium*	Wild morning-glory
	Corallorhiza	*trifida*	Early coralroot
	Cornus	*canadensis*	Bunchberry
	Disporum	*trachycarpum*	Fairybells
	Elymus	*species*	Wild rye
	Equisetum	*pratense*	Meadow horsetail
	Fragaria	*virginiana*	Strawberry
	Galium	*boreale*	Northern bedstraw
	Galium	*triflorum*	Sweet-scented bedstraw
	Galium	*trifidum*	Small bedstraw
	Heracleum	*lanatum*	Cow-parsnip
	Houstonia	*longifolia*	Bluets
	Lathyrus	*ochroleucus*	Creamy peavine
	Lathyrus	*palustris*	Marsh vetchling
	Lathyrus	*venosus*	Wild peavine
	Lilium	*philadelphicum*	Tiger lily
	Lysimachia	*ciliata*	Fringed loosestrife
	Maianthemum	*canadense*	Wild lily-of-the-valley

Plant Form	Genus	Species	Common Name
	Matteuccia	*struthopteris*	Ostrich fern
	Melilotus	*officinalis*	Yellow sweet clover
	Milium	*effusum*	Millet grass
	Mentha	*arvensis*	Field mint
	Mertensia	*paniculata*	Tall lungwort
	Mitella	*nuda*	Bishop's cap
	Monarda	*fistula*	Wild bergamot
	Monotropa	*hypopithys*	Pinesap
	Oryzopsis	*asperifolia*	Rice grass
	Osmorhiza	*longistylis*	Sweet cicely
	Petasites	*palmatus*	Palmate-leaved colt's-foot
	Petasites	*sagittatus*	Arrow-leaved colt's-foot
	Poa	*pratensis*	Kentucky blue grass
	Pyrola	*asarifolia*	Pink wintergreen
	Pyrola	*elliptica*	Shinleaf
	Pyrola	*secunda*	One-sided wintergreen
	Rubus	*pubescens*	Dewberry
	Rudbeckia	*laciniata*	Tall coneflower
	Rudbeckia	*serotina*	Black-eyed Susan
	Sanicula	*marilandica*	Snakeroot
	Schizachne	*purpurascens*	Purple oat grass
	Sisyrinchium	*montanum*	Blue-eyed-grass
	Smilacina	*stellata*	Star-flowered Solomon's seal
	Smilax	*herbacea*	Carrionflower
	Solidago	*canadensis*	Canada goldenrod
	Sonchus	*arvensis*	Perennial sowthistle
	Taraxacum	*officinale*	Dandelion
	Thalictrum	*dasycarpum*	Tall meadow-rue
	Thalictrum	*venulosum*	Veiny meadow-rue
	Trifolium	*repens*	White clover
	Trillium	*cernuum*	Nodding trillium
	Vicia	*americana*	American vetch
	Viola	*rugulosa*	Western Canada violet
	Viola	*species*	Violet species
Mosses	*Bracathecium*	*species*	Feather moss
	Hypnum	*species*	Pigtail moss
	Mnium	*species*	Leafy moss
	Haplocladium	*species*	Haplocladium
	Anomodon	*species*	Anomodon

APPENDIX 2

Lowess Curve Figures

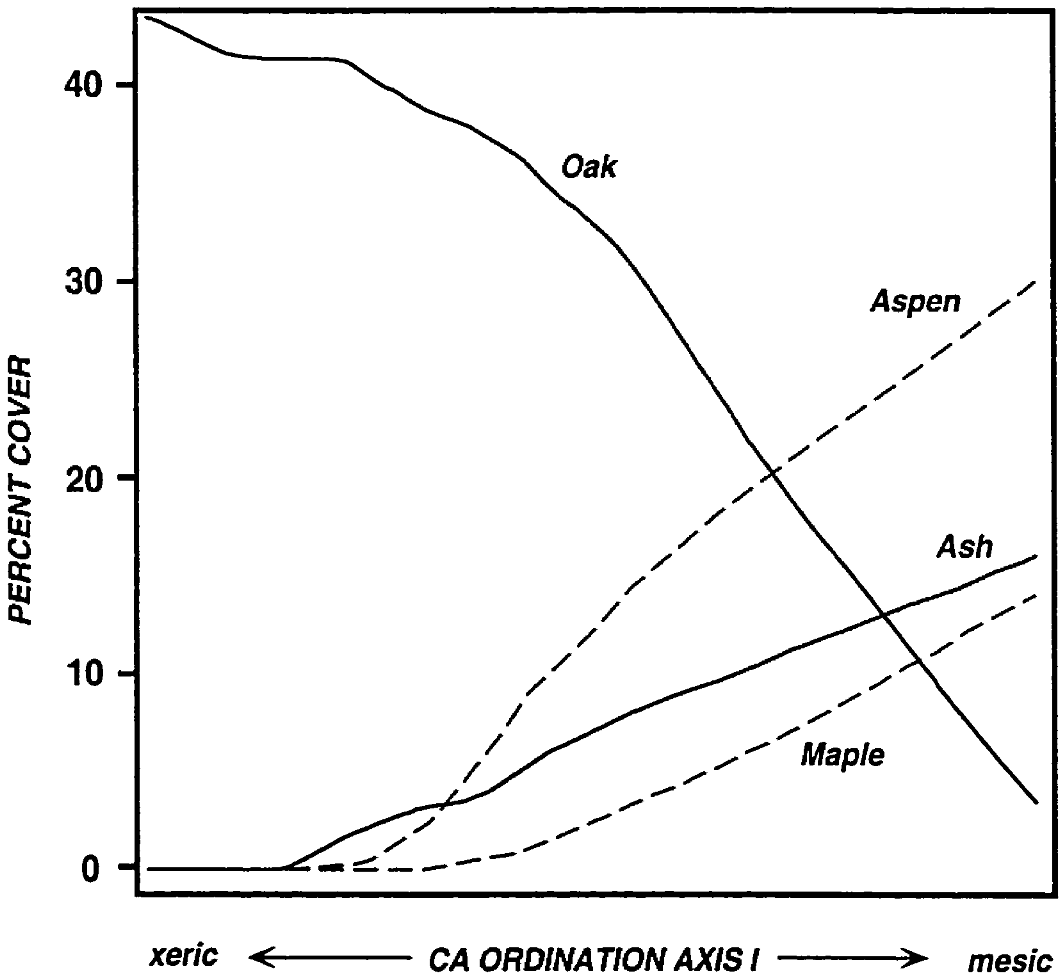
APPENDIX 2a. Changes in abundance of main tree species along the first CA ordination axis, which is interpreted as a soil moisture gradient.

APPENDIX 2b. Changes in abundance of major tall species along the first CA ordination axis, which is interpreted as a soil moisture gradient.

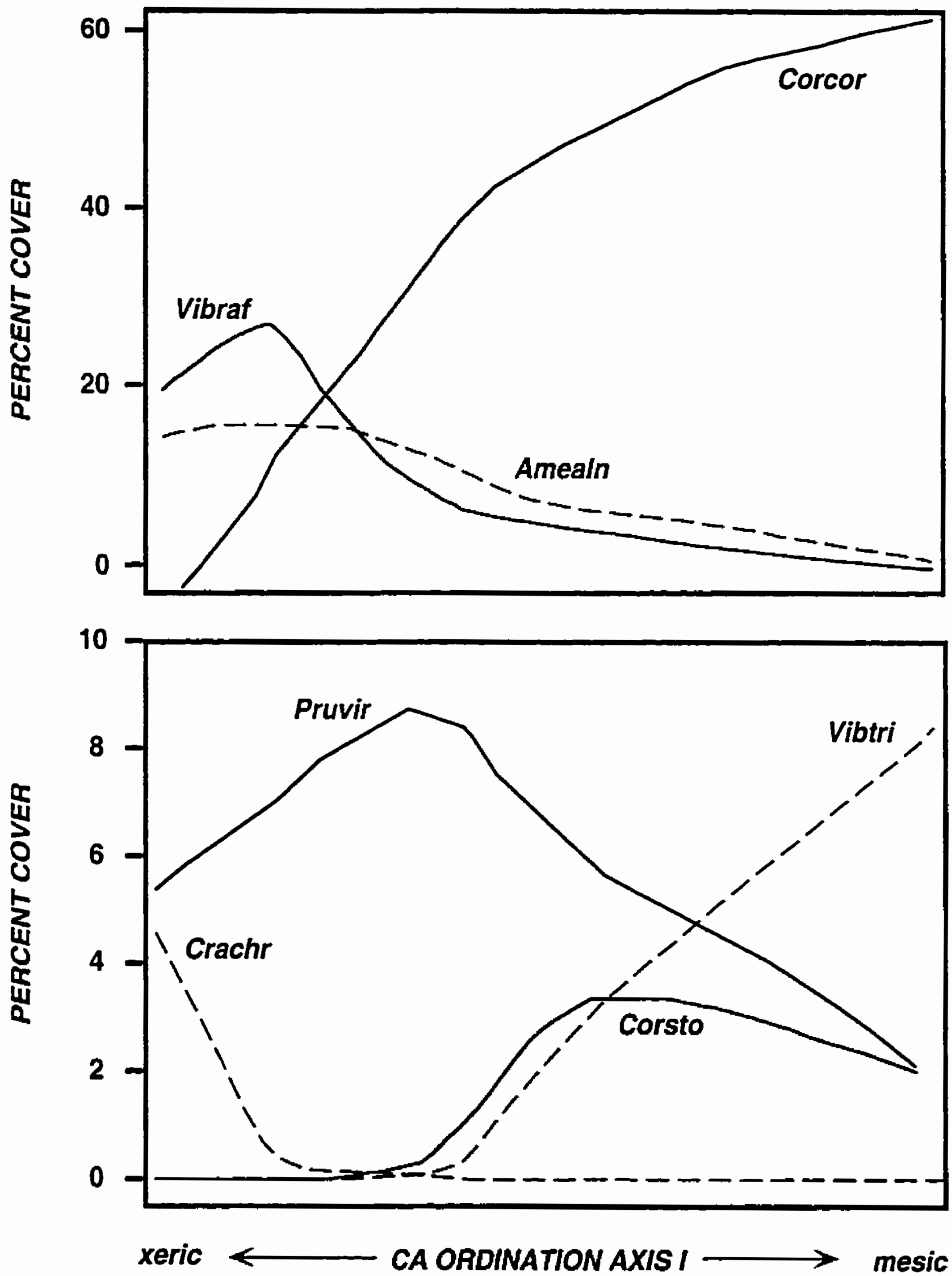
APPENDIX 2c. Changes in abundance of major low-statured shrubs along the first CA ordination axis, which is interpreted as a soil moisture gradient.

APPENDIX 2d. Changes in abundance of major herbaceous species along the first CA ordination axis, which is interpreted as a soil moisture gradient.

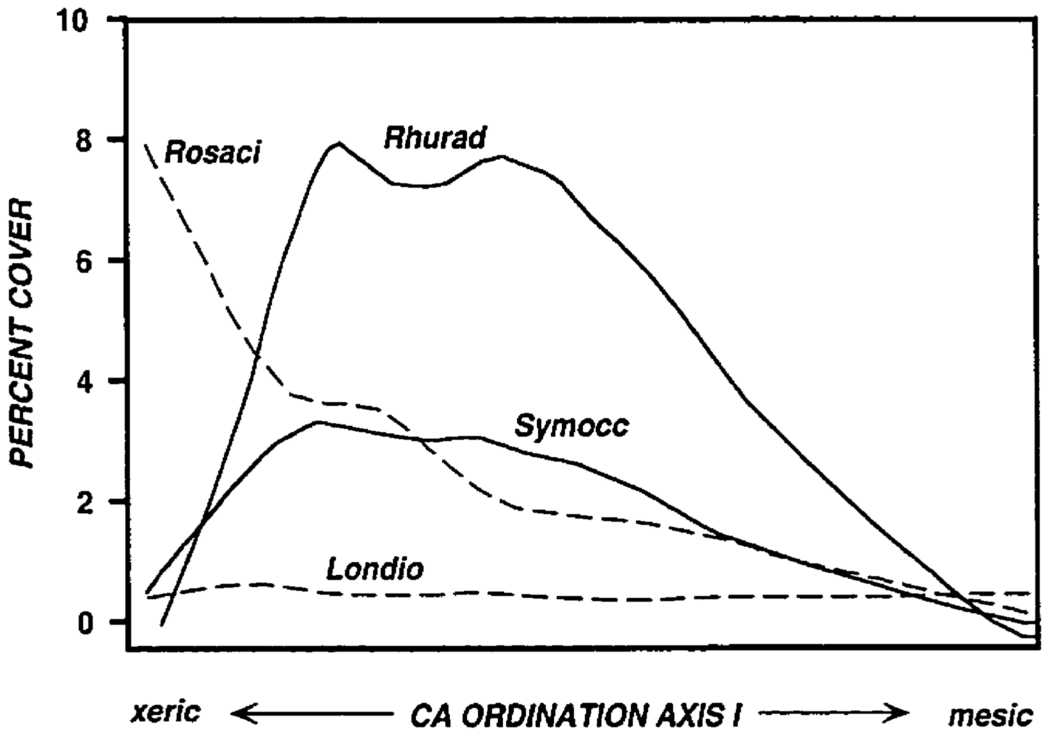
APPENDIX 2e. Changes in abundance of plant functional groups along the first CA ordination axis, which is interpreted as a soil moisture gradient.



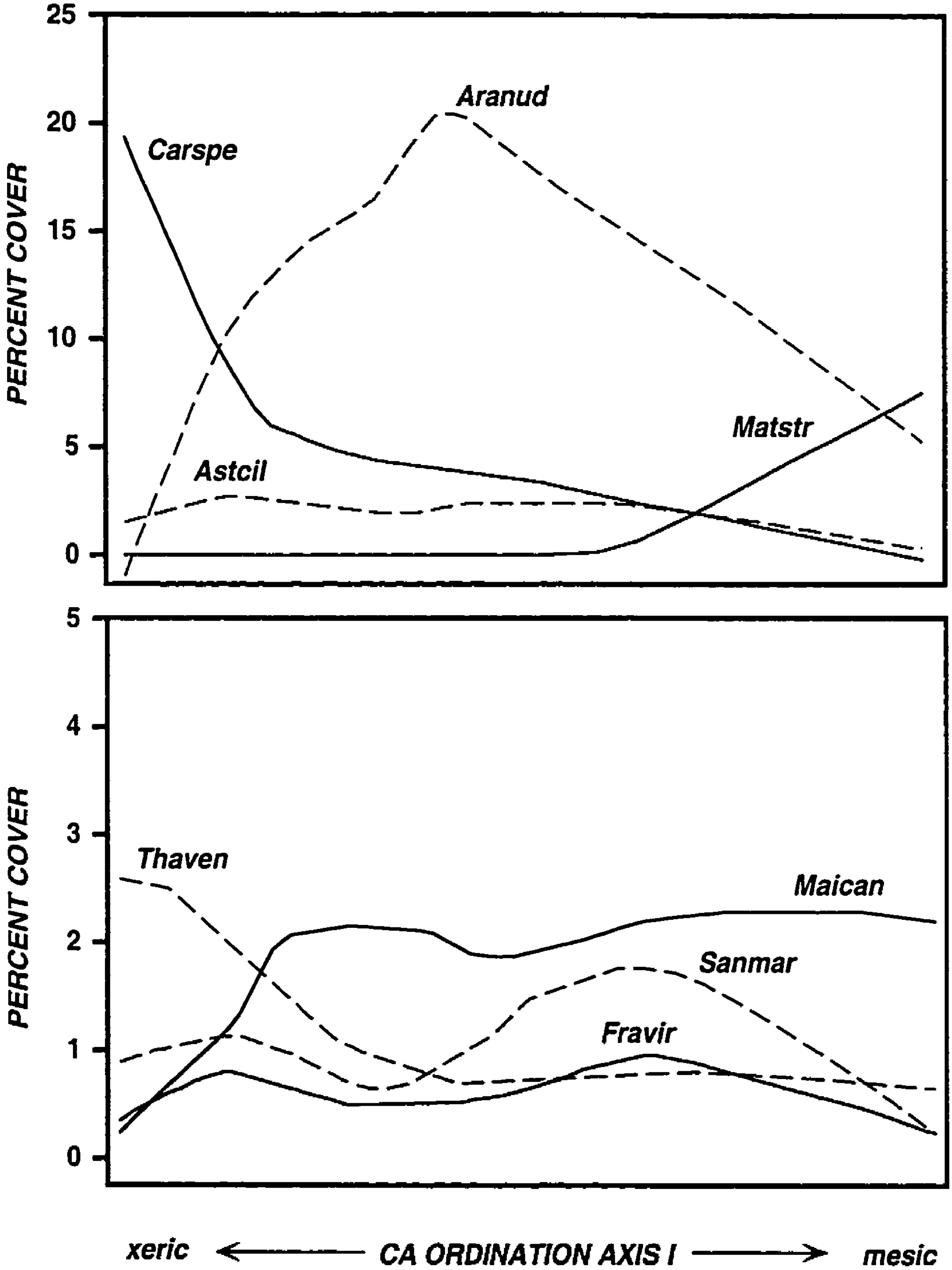
Appendix 2a. Changes in adundance of main tree species along the first CA ordination axis, which is interpreted as a soil moisture gradient. Data fitted using lowess curves. Refer to text for details.



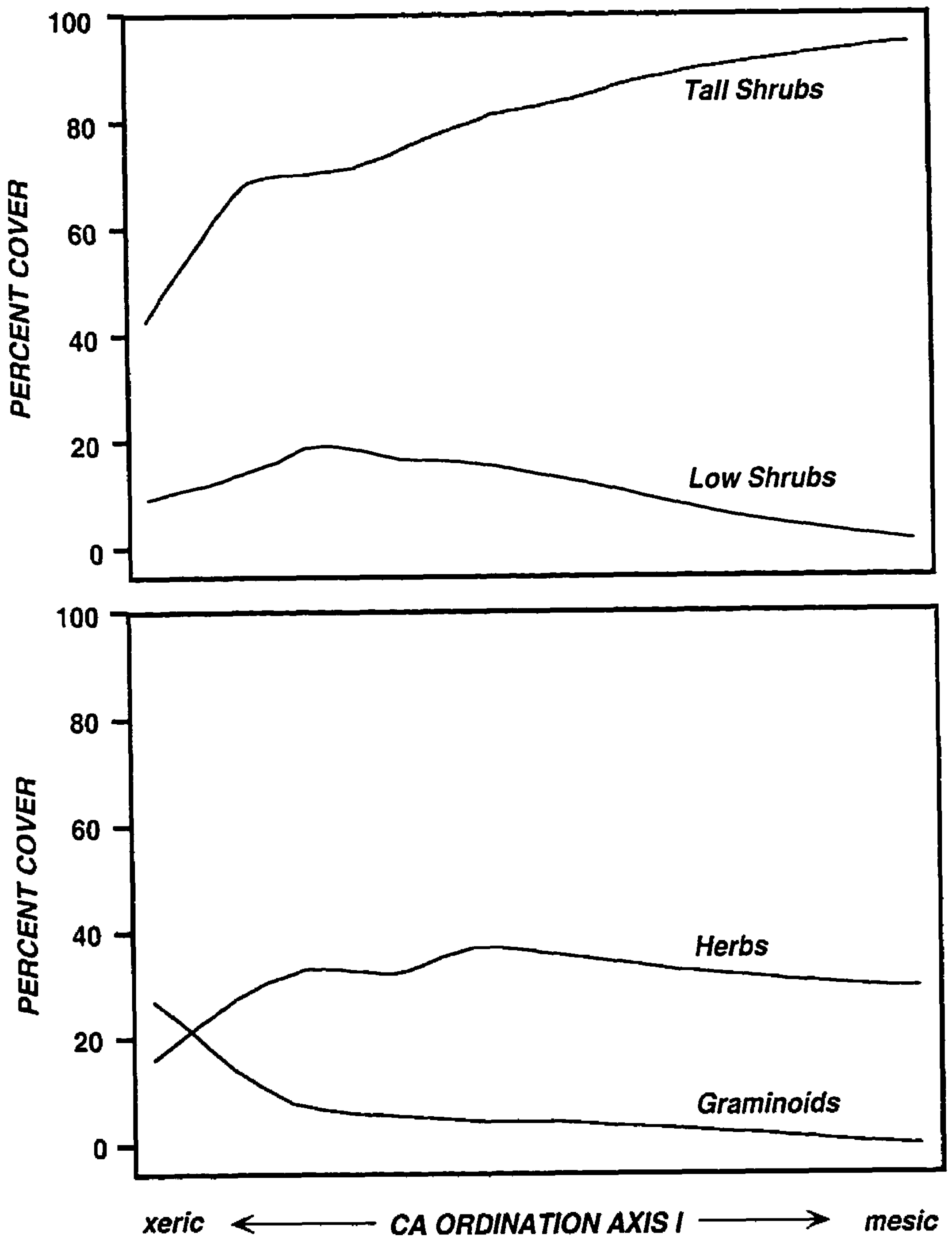
Appendix 2b. Changes in adundance of major tall species along the first CA ordination axis, which is interpreted as a soil moisture gradient. Data fitted using lowess curves. Refer to text for details. Species: *Vibraf* = arrowwood; *Amealn* = saskatoon berry; *Corcor* = hazelnut; *Crachr* = hawthrorn: *Pruvir* = chokecherry; *Corsto* = red-osier dogwood; *Vibtri* = highbush cranberry.



Appendix 2c. Changes in adundance of major low-statured shrubs along the first CA ordination axis, which is interpreted as a soil moisture gradient. Data fitted using lowess curves. Refer to text for details. Species: Rosaci = rose; Londio = honeysuckle; Rhurad = poison ivy; Symocc = snowberry.



Appendix 2d. Changes in adundance of major herbaceous species along the first CA ordination axis, which is interpreted as a soil moisture gradient. Data fitted using lowess curves. Refer to text for details. Species: *Carspe* = sedges; *Astcil* = aster; *Aranud* = wild sarsaparilla; *Matstr* = ostrich fern; *Thaven* = meadow rue; *Fravir* = strawberry; *Sanmar* = snakeroot; *Maican* = lily of the valley.



Appendix 2e. Changes in adundance of plant functional groups along the first CA ordination axis, which is interpreted as a soil moisture gradient. Data fitted using lowess curves. Refer to text for details.

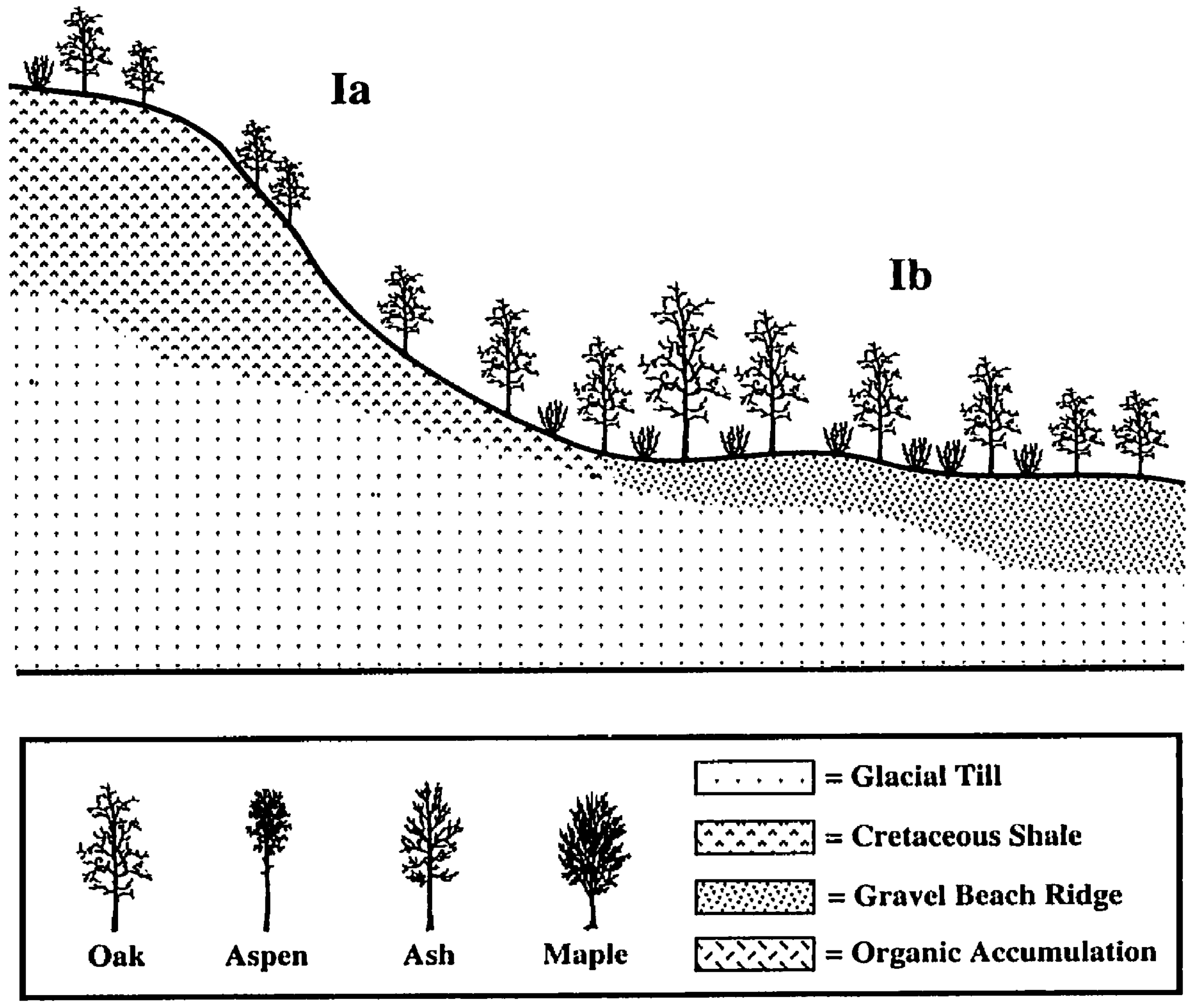
APPENDIX 3

Physiognomic Profiles for Stand Types

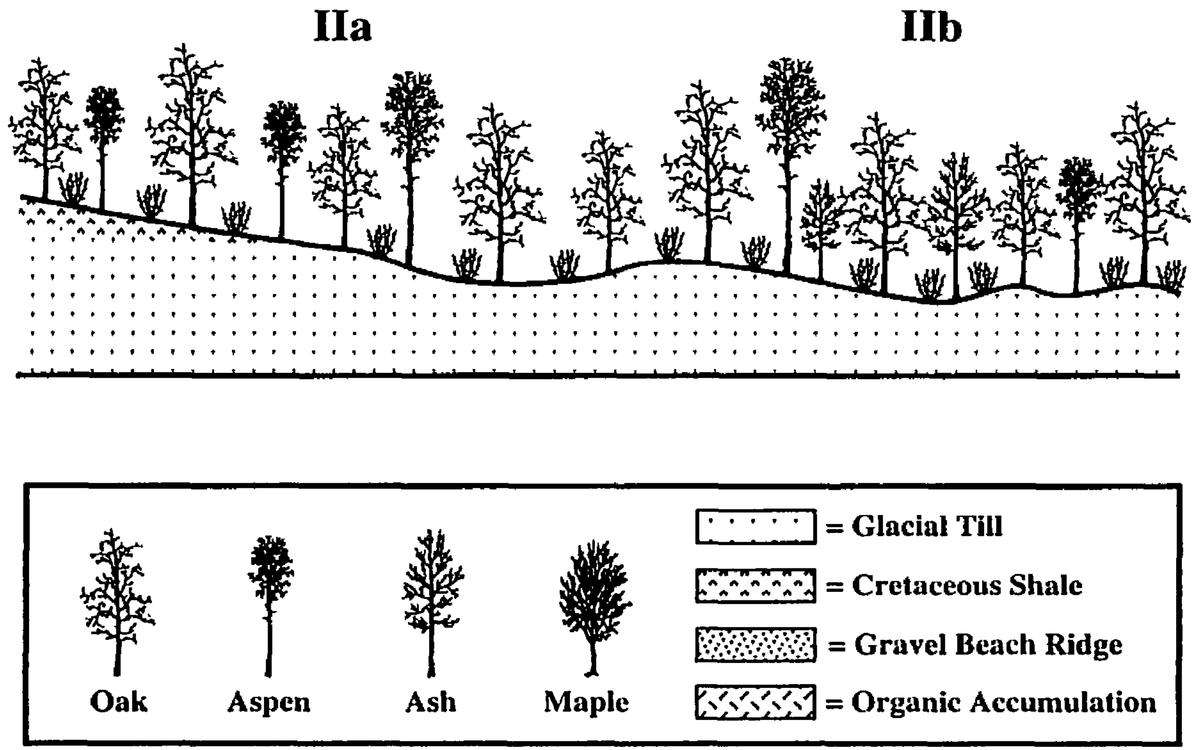
APPENDIX 3a. Idealized physiognomic-physiographic profile of stand type I (Bur Oak - Low Shrub).

APPENDIX 3b. Idealized physiognomic-physiographic profile of stand type II (Bur Oak - Tall Shrub).

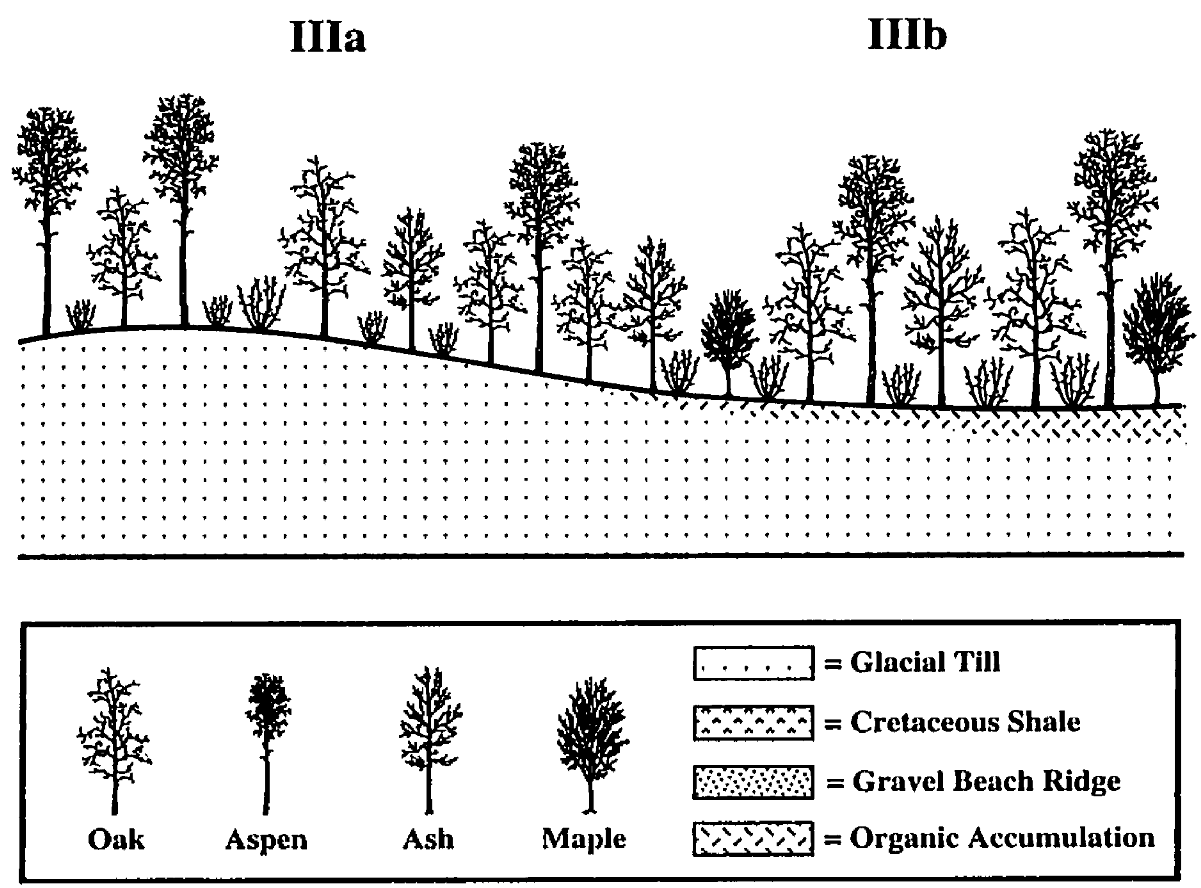
APPENDIX 3c. Idealized physiognomic-physiographic profile of stand type III (Oak - Aspen - Ash).



Appendix 3a. Idealized physiognomic-physiographic profile of stand type I (Bur Oak - Low Shrub).



Appendix 3b. Idealized physiognomic-physiographic profile of stand type II (Bur Oak - Tall Shrub).



Appendix 3c. Idealized physiognomic-physiographic profile of stand type III (Oak - Aspen - Ash).

APPENDIX 4

Stand Type I Tables

APPENDIX 4a. STAND TYPE I. Relative frequency of tree species in canopies 1 - 5.

APPENDIX 4b. STAND TYPE I. Frequency, mean cover and variance of tree species.

APPENDIX 4c. STAND TYPE I. Mean basal area per $100m^2$ for canopies 1 - 4.

APPENDIX 4d. STAND TYPE I. Mean density per $100m^2$ for canopies 1 - 5.

APPENDIX 4e. STAND TYPE I. Frequency, mean cover and variance of common shrubs (f>5%).

APPENDIX 4f. STAND TYPE I. Frequency, mean cover and variance of common herbs and moss species (*f*>5%).

APPENDIX 4g. STAND TYPE IA. Relative frequency of trees.

APPENDIX 4h. STAND TYPE IB. Relative frequency of trees.

APPENDIX 4i. STAND TYPE IA. Mean Density and frequency of seedlings and suckers per plot.

APPENDIX 4j. STAND TYPE IB. Mean Density and frequency of seedlings and suckers per plot.

APPENDIX 4a. STAND TYPE I. Relative frequency of tree species in canopies 1 - 5.

Species	Common name	Canopy layer				
		Total	1	2	3	4
Abies balsamea	Balsam fir	0.03	-	-	0.01	0.01
Fraxinus pennsylvanica	Green ash	0.08	-	0.01	0.06	0.01
Picea glauca	White spruce	0.03	0.01	-	0.01	-
Populus tremuloides	Trembling aspen	0.08	-	0.01	0.06	0.03
Quercus macrocarpa	**Bur oak**	**1.00**	-	**0.27**	**0.96**	**0.39**

APPENDIX 4b. STAND TYPE I. Frequency, mean cover and variance of tree species.

Species	Common name	Frequency	Mean Cover (%)	Variance
Abies balsamea	Balsam fir	0.03	0.08	0.33
Fraxinus pennsylvanica	Green Ash	0.08	0.84	15.26
Picea glauca	White spruce	0.03	0.19	1.57
Populus tremuloides	Trembling aspen	0.08	0.25	2.89
Quercus macrocarpa	**Bur oak**	**1.00**	**40.94**	**165.10**

APPENDIX 4c. STAND TYPE I. Mean basal area per 100m² for each tree species in canopies 1 - 4.

Species	Common name	Canopy layer				
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Fraxinus pennsylvanica	Green ash	0.001	-	-	0.001	-
Picea glauca	White spruce	0.002	0.002	-	-	-
Populus tremuloides	Trembling aspen	-	-	-	-	-
Quercus macrocarpa	Bur oak	0.200	-	0.045	0.153	0.003

APPENDIX 4d. STAND TYPE I. Mean density per 100m² for each tree species in canopies 1 - 5.

Species	Common name	Canopy layer					
		Total	1	2	3	4	5
Abies balsamea	Balsam fir	0.38	-	-	0.05	0.01	0.32
Fraxinus pennsylvanica	Green ash	0.53	-	0.01	0.14	0.03	0.35
Picea glauca	White spruce	0.03	0.01	-	0.01	-	-
Populus tremuloides	Trembling aspen	0.28	-	0.03	0.08	0.03	0.15
Quercus macrocarpa	Bur oak	35.34	-	1.22	13.57	3.63	16.92

APPENDIX 4e. STAND TYPE I. Frequency, mean cover and variance of common shrubs (f>5%).

Species	Common name	Frequency	Mean Cover (%)	Variance
Amelanchier alnifolia	Saskatoonberry	1.00	18.49	261.02
Symphoricarpos occidentalis	Wolfberry	0.97	3.59	31.88
Viburnum rafinesquianum	Downy arrowwood	0.95	27.09	456.64
Prunus virginiana	Chokecherry	0.90	7.63	49.22
Rosa acicularis	Prickly rose	0.89	5.40	40.07
Lonicera dioica	Twining honeysuckle	0.75	0.71	0.68
Corylus cornuta	Beaked hazelnut	0.63	11.75	209.89
Rhus radicans	Poison ivy	0.61	5.53	134.40
Crataegus chrysocarpa	Hawthorn	0.38	1.54	11.60
Symphoricarpos albus	Snowberry	0.14	0.08	0.07
Prunus pensylvanica	Pin cherry	0.13	0.65	5.55
Diervilla lonicera	Bush-honeysuckle	0.11	0.05	0.02
Rubus idaeus	Raspberry	0.10	0.03	0.01
Prunus americana	Wild plum	0.05	0.13	0.42
Shepherdia canadensis	Buffaloberry	0.05	0.09	0.21
Viburnum lentago	Nannyberry	0.05	0.97	28.75

APPENDIX 4f. STAND TYPE I. Frequency, mean cover and variance of common herbs and moss species (f>5%).

Species	Common Name	Frequency	Mean Cover (%)	Variance
Carex peckii/pensylvanica	Carex species	0.99	9.21	72.19
Thalictrum venulosum	Veiny meadow-rue	0.92	2.08	1.91
Galium boreale	Northern bedstraw	0.89	0.91	0.64
Aster ciliolatus	Lindley's aster	0.87	2.69	5.90
Sanicula marilandica	Snakeroot	0.82	1.32	1.97
Maianthemum canadense	Wild lily-of-the-valley	0.80	1.58	2.56
Aralia nudicaulis	Wild sarsaparilla	0.78	11.72	165.00
Oryzopsis asperifolia	Rice grass	0.73	2.12	5.07
Lathyrus venosus	Wild peavine	0.72	2.60	52.92
Fragaria virginiana	Strawberry	0.62	0.92	1.50
Solidago canadensis	Canada goldenrod	0.51	1.31	6.42
Lathyrus ochroleucus	Creamy peavine	0.49	0.66	1.47
Lysimachia ciliata	Fringed loosestrife	0.38	0.33	0.47
Vicia americana	American vetch	0.37	0.31	0.44
Apocynum androsaemifolium	Spreading dogbane	0.29	0.58	1.88
Monarda fistulosa	Wild bergamot	0.29	0.41	1.14
Viola species	Violet species	0.25	0.43	1.39
Elymus species	Wildrye	0.20	0.13	0.13
Osmorhiza longistylis	Sweet cicely	0.20	0.13	0.14
Agastache foeniculum	Giant-hyssop	0.15	0.25	0.74
Bromus species	Brome species	0.15	0.43	3.32
Achillea millifolium	Yarrow	0.14	0.08	0.10
Smilax herbacea	Carrionflower	0.14	0.22	0.89
Bromus inermus	Brome grass	0.13	0.10	0.26
Anemomne quinquefolia	Wood anemone	0.10	0.07	0.15
Thalictrum dasycarpum	Tall meadow-rue	0.10	0.34	1.75
Pyrola asarifolia	Pink wintergreen	0.09	0.06	0.05
Comandra umbellata	Bastard toadflax	0.08	0.06	0.06
Poa pratensis	Kentucky blue grass	0.06	0.04	0.04
Taraxacum officinale	Dandelion	0.06	0.03	0.03
Schizachne purpurascens	Purple oat grass	0.05	0.01	0.00
Mosses				
Brachythecium species	Feather mosses	0.05	0.02	0.01
Mnium species	Leafy mosses	0.05	0.10	0.51

APPENDIX 4g. STAND TYPE IA. Relative frequency of trees.

Species	Common name			Canopy layer		
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Fraxinus pennsylvanica	Green ash	0.08	-	-	0.08	0.03
Picea glauca	White spruce	-	-	-	-	-
Populus tremuloides	Trembling aspen	0.08	-	0.03	0.05	0.05
Quercus macrocarpa	**Bur oak**	**1.00**	-	**0.13**	**1.00**	**0.45**

APPENDIX 4h. STAND TYPE IB. Relative frequency of trees.

Species	Common name			Canopy layer		
		Total	1	2	3	4
Abies balsamea	Balsam fir	0.05	-	-	0.02	0.02
Fraxinus pennsylvanica	Green ash	0.07	-	0.02	0.05	-
Picea glauca	White spruce	0.05	0.02	-	0.02	-
Populus tremuloides	Trembling aspen	0.07	-	-	0.07	-
Quercus macrocarpa	**Bur oak**	**1.00**	-	**0.39**	**0.93**	**0.34**

APPENDIX 4i. STAND TYPE IA. Mean Density and frequency of seedlings and suckers per plot.

Species	Common name	Seedlings		Suckers	
		Frequency	Density	Frequency	Density
Abies balsamea	Balsam fir	-	-	-	-
Fraxinus pennsylvanica	Green ash	0.11	0.55	0.03	0.08
Picea glauca	White spruce	-	-	-	-
Populus tremuloides	Trembling aspen	-	-	0.03	0.08
Quercus macrocarpa	**Bur oak**	**0.87**	**7.26**	**0.84**	**11.16**

APPENDIX 4j. STAND TYPE IB. Mean Density and frequency of seedlings and suckers per plot.

Species	Common name	Seedlings		Suckers	
		Frequency	Density	Frequency	Density
Abies balsamea	Balsam fir	0.70	0.42	0.02	0.20
Fraxinus pennsylvanica	Green ash	0.30	0.30	0.02	0.07
Picea glauca	White spruce	-	-	-	-
Populus tremuloides	Trembling aspen	-	-	0.12	0.15
Quercus macrocarpa	**Bur oak**	**0.95**	**7.00**	**0.71**	**8.54**

APPENDIX 5

Stand Type II Tables

APPENDIX 5a. STAND TYPE II. Relative frequency of tree species for canopies 1-4.

APPENDIX 5b. STAND TYPE II. Frequency, mean cover and variance of tree species.

APPENDIX 5c. STAND TYPE II. Mean basal area per $100m^2$ for each tree species in canopies 1-4.

APPENDIX 5d. STAND TYPE II. Mean density per $100m^2$ for each tree species in canopies 1-5.

APPENDIX 5e. STAND TYPE II. Frequency, mean cover and variance of common shrubs (f>5%).

APPENDIX 5f. STAND TYPE II. Frequency, mean cover and variance of common herb species (f>5%).

APPENDIX 5g. STAND TYPE IIA. Relative frequency of tree species in canopies 1-4.

APPENDIX 5h. STAND TYPE IIB. Relative frequency of tree species in canopies 1-4.

APPENDIX 5i. STAND TYPE IIA. Mean Density and frequency of seedlings and suckers per plot.

APPENDIX 5j. STAND TYPE IIB. Mean Density and frequency of seedlings and suckers per plot.

APPENDIX 5a. STAND TYPE II. Relative frequency of tree species for canopies 1-4.

Species	Common name	Canopy layer				
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Acer negundo	Manitoba maple	0.12	-	0.01	0.08	0.04
Betula papyrifera	Paper birch	0.05	-	0.04	0.01	-
Fraxinus pennsylvanica	Green ash	0.58	0.04	0.32	0.40	0.16
Picea glauca	White spruce	0.05	0.04	0.01	0.01	0.01
Populus balsamifera	Balsam poplar	0.08	0.12	0.04	0.01	-
Populus tremuloides	Trembling aspen	0.41	0.03	0.23	0.16	-
Quercus macrocarpa	**Bur oak**	**1.00**	-	**0.68**	**0.89**	**0.15**
Ulmus americana	American elm	0.07	-	-	0.04	0.03

APPENDIX 5b. STAND TYPE II. Frequency, mean cover and variance of tree species.

Species	Common name	Frequency	Mean Cover (%)	Variance
Abies balsamea	Balsam fir	-	-	-
Acer negundo	Manitoba maple	0.12	0.47	2.75
Betula papyrifera	Paper birch	0.05	0.82	18.07
Fraxinus pennsylvanica	Green Ash	0.58	6.96	77.38
Picea glauca	White spruce	0.05	0.76	11.01
Populus balsamifera	Balsam poplar	0.08	1.51	29.64
Populus tremuloides	Trembling aspen	0.41	6.42	129.52
Quercus macrocarpa	**Bur oak**	**1.00**	**36.64**	**243.52**
Ulmus americana	American Elm	0.07	0.09	0.13

APPENDIX 5c. STAND TYPE II. Mean basal area per 100m² for each tree species in canopies 1-4.

Species	Common name		Canopy layer			
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Acer negundo	Manitoba maple	-	-	-	-	-
Betula papyrifera	Paper birch	0.010	0.006	0.004	0.002	-
Fraxinus pennsylvanica	Green ash	0.025	-	0.014	0.010	-
Picea glauca	White spruce	0.009	0.008	0.001	-	-
Populus balsamifera	Balsam poplar	0.002	0.002	-	-	-
Populus tremuloides	Trembling aspen	0.040	0.028	0.010	0.002	-
Quercus macrocarpa	**Bur oak**	**0.171**	-	**0.111**	**0.059**	-
Ulmus americana	American elm	-	-	-	-	-

APPENDIX 5d. STAND TYPE II. Mean density per 100m² for each tree species in canopies 1-5.

Species	Common name		Canopy layer				
		Total	1	2	3	4	5
Abies balsamea	Balsam fir	1.85	-	-	-	-	1.85
Acer negundo	Manitoba maple	0.52	-	0.01	0.16	0.18	0.16
Betula papyrifera	Paper birch	0.12	0.03	0.05	-	-	0.04
Fraxinus pennsylvanica	Green ash	5.27	-	0.53	1.48	0.36	2.90
Picea glauca	White spruce	0.18	0.05	0.03	0.05	0.01	0.03
Populus balsamifera	Balsam poplar	0.36	0.04	0.12	0.07	-	0.12
Populus tremuloides	Trembling aspen	2.16	0.33	0.53	0.37	-	0.93
Quercus macrocarpa	**Bur oak**	**17.97**	**0.01**	**3.34**	**7.81**	**0.42**	**6.38**
Ulmus americana	American elm	0.34	-	0.03	0.04	-	0.27

APPENDIX 5e. STAND TYPE II. Frequency, mean cover and variance of common shrubs (f>5%).

Species	Common name	Frequency	Mean Cover (%)	Variance
Corylus cornuta	Beaked hazelnut	0.99	38.27	473.96
Amelanchier alnifolia	Saskatoonberry	0.95	11.52	114.12
Symphoricarpos occidentalis	Wolfberry	0.95	3.81	10.67
Rhus radicans	Poison ivy	0.93	14.85	244.28
Prunus virginiana	Chokecherry	0.88	9.05	69.86
Viburnum rafinesquianum	Downy arrowwood	0.85	8.14	90.86
Rosa acicularis	Prickly rose	0.77	5.73	111.01
Lonicera dioica	Twining honeysuckle	0.51	0.48	0.57
Cornus stolonifera	Dogwood	0.37	3.02	46.95
Viburnum trilobum	High bush-cranberry	0.30	1.06	5.75
Rubus idaeus	Raspberry	0.23	0.16	0.32
Viburnum lentago	Nannyberry	0.21	2.55	60.78
Prunus pensylvanica	Pin cherry	0.18	1.71	23.08
Crataegus chrysocarpa	Hawthorn	0.14	0.37	1.57
Diervilla lonicera	Bush-honeysuckle	0.12	0.13	0.17
Symphoricarpos albus	Snowberry	0.12	0.07	0.08
Acer spicatum	Mountain maple	0.10	0.38	2.51
Ribes triste	Red currant	0.05	0.05	0.05

APPENDIX 5f. STAND TYPE II. Frequency, mean cover and variance of common herb species (f>5%).

Species	Common Name	Frequency	Mean Cover (%)	Variance
Maianthemum canadense	Wild lily-of-the-valley	0.95	2.36	3.79
Aralia nudicaulis	Wild sarsaparilla	0.93	22.15	319.78
Carex peckii/pensylvanica	Carex species	0.89	4.90	29.93
Aster ciliolatus	Lindley's aster	0.84	2.72	7.70
Oryzopsis asperifolia	Rice grass	0.82	1.22	1.72
Thalictrum venulosum	Veiny meadow-rue	0.68	0.90	1.30
Galium boreale	Northern bedstraw	0.64	0.38	0.22
Sanicula marilandica	Snakeroot	0.63	1.31	3.68
Lathyrus venosus	Wild peavine	0.52	0.90	2.83
Fragaria virginiana	Strawberry	0.51	0.96	2.61
Solidago canadensis	Canada goldenrod	0.48	1.56	11.59
Viola species	Violet species	0.36	0.28	0.30
Thalictrum dasycarpum	Tall meadow-rue	0.27	0.92	5.09
Osmorhiza longistylis	Sweet cicely	0.23	0.26	0.58
Pyrola asarifolia	Pink wintergreen	0.23	0.19	0.17
Galium triflorum	Sweet scented bedstraw	0.22	0.14	0.14
Apocynum androsaemifolium	Spreading dogbane	0.18	0.47	2.16
Lathyrus ochroleucus	Creamy peavine	0.16	0.13	0.14
Rubus pubescens	Dewberry	0.16	0.26	0.59
Smilacina stellata	Star-flowered Solomon's seal	0.16	0.13	0.11
Anemomne quinquefolia	Wood anemone	0.15	0.08	0.05
Lysimachia ciliata	Fringed loosestrife	0.14	0.15	0.21
Disporum trachycarpum	Fairybells	0.12	0.16	0.25
Vicia americana	American vetch	0.12	0.07	0.04
Heracleum lanatum	Cow parsnip	0.10	0.42	3.09
Rudbeckia laciniata	Tall coneflower	0.10	0.33	2.43
Smilax herbacea	Carrionflower	0.10	0.13	0.26
Amphicarpa bracteata	Hog-peanut	0.08	0.12	0.24
Bromus inermus	Brome grass	0.08	0.03	0.01
Trillium cernuum	Nodding trillium	0.08	0.08	0.10
Achillea millifolium	Yarrow	0.05	0.02	0.01
Sonchus arvensis	Perennial sowthistle	0.05	0.03	0.02
Mosses				
Brachythecium species	Feather mosses	0.18	0.20	0.23
Mnium species	Leafy mosses	0.10	0.13	0.25

APPENDIX 5g. STAND TYPE IIA. Relative frequency of tree species in canopies 1-4.

Species	Common name	Canopy layer				
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Acer negundo	Manitoba maple	0.06	-	-	0.02	0.06
Betula papyrifera	Paper birch	0.08	-	0.06	0.02	-
Fraxinus pennsylvanica	Green ash	0.42	-	0.16	0.28	0.14
Picea glauca	White spruce	0.06	0.04	0.02	0.02	0.02
Populus balsamifera	Balsam poplar	-	-	-	-	-
Populus tremuloides	Trembling aspen	0.44	0.10	0.26	0.22	-
Quercus macrocarpa	**Bur oak**	**1.00**	**0.02**	**0.66**	**0.94**	**0.20**
Ulmus americana	American elm	0.06	-	-	0.02	0.04

APPENDIX 5h. STAND TYPE IIB. Relative frequency of tree species in canopies 1-4.

Species	Common name	Canopy layer				
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Acer negundo	Manitoba maple	0.26	-	0.04	0.22	-
Betula papyrifera	Paper birch	-	-	-	-	-
Fraxinus pennsylvanica	Green ash	0.91	-	0.65	0.65	0.22
Picea glauca	White spruce	0.04	0.04	-	-	-
Populus balsamifera	Balsam poplar	0.26	0.13	0.13	0.04	-
Populus tremuloides	Trembling aspen	0.35	0.17	0.17	0.04	-
Quercus macrocarpa	**Bur oak**	**1.00**	**0.04**	**0.74**	**0.78**	**0.04**
Ulmus americana	American elm	0.09	-	-	0.09	-

APPENDIX 5i. STAND TYPE IIA. Mean Density and frequency of seedlings and suckers per plot.

Species	Common name	Seedlings		Suckers	
		Frequency	Density	Frequency	Density
Abies balsamea	Balsam fir	0.06	2.24	-	-
Acer negundo	Manitoba maple	0.06	0.08	0.04	0.14
Betula papyrifera	Paper birch	0.04	0.04	-	-
Fraxinus pennsylvanica	Green ash	0.22	0.58	0.14	0.54
Picea glauca	White spruce	0.02	0.04	-	-
Populus balsamifera	Balsam poplar	0.02	0.14	-	-
Populus tremuloides	Trembling aspen	-	-	0.34	0.84
Quercus macrocarpa	**Bur oak**	**0.88**	**4.30**	**0.28**	**2.22**
Ulmus americana	Elm	-	-	0.02	0.12

APPENDIX 5j. STAND TYPE IIB. Mean Density and frequency of seedlings and suckers per plot.

Species	Common name	Seedlings		Suckers	
		Frequency	Density	Frequency	Density
Abies balsamea	Balsam fir	0.13	1.00	-	-
Acer negundo	Manitoba maple	0.04	0.04	-	-
Betula papyrifera	Paper birch	0.04	0.04	-	-
Fraxinus pennsylvanica	Green ash	0.57	3.65	0.22	3.13
Picea glauca	White spruce	-	-	-	-
Populus balsamifera	Balsam poplar	0.04	0.09	-	-
Populus tremuloides	Trembling aspen	-	-	0.35	1.04
Quercus macrocarpa	**Bur oak**	**0.87**	**4.04**	**0.43**	**2.04**
Ulmus americana	Elm	0.17	0.17	0.04	0.43

APPENDIX 6

Stand Type III Tables

APPENDIX 6a. STAND TYPE III. Relative frequency of tree species in canopies 1-4.

APPENDIX 6b. STAND TYPE III. Frequency, mean cover and variance of tree species.

APPENDIX 6c. STAND TYPE III. Mean basal area per 100 m^2 for each tree species in canopies 1-4.

APPENDIX 6d. STAND TYPE III. Mean density per 100 m^2 for each tree species in canopies 1-5.

APPENDIX 6e. STAND TYPE III. Frequency, mean cover and variance of common shrubs (f>5%).

APPENDIX 6f. STAND TYPE III. Frequency, mean cover and variance of common herb species (f>5%).

APPENDIX 6g. STAND TYPE IIIA. Relative frequency of tree species for each tree species in canopies 1-4.

APPENDIX 6h. STAND TYPE IIIB. Relative frequency of tree species for each tree species in canopies 1-4.

APPENDIX 6i. STAND TYPE IIIA. Mean Density and frequency of seedlings and suckers per plot.

APPENDIX 6j. STAND TYPE IIIB. Mean Density and frequency of seedlings and suckers per plot.

APPENDIX 6a. STAND TYPE III. Relative frequency of tree species in canopies 1-4.

Species	Common name	Canopy layer				
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Acer negundo	Manitoba maple	0.64	0.05	0.33	0.54	0.18
Betula papyrifera	Paper birch	0.13	-	0.05	0.13	-
Fraxinus pennsylvanica	Green ash	0.90	0.05	0.51	0.69	0.31
Picea glauca	White spruce	-	-	-	-	-
Populus balsamifera	Balsam poplar	-	-	-	-	-
Populus tremuloides	Trembling aspen	0.82	0.74	0.15	0.18	0.05
Quercus macrocarpa	**Bur oak**	**1.00**	-	**0.79**	**0.56**	**0.08**
Ulmus americana	American elm	0.28	0.05	0.15	0.18	0.08

APPENDIX 6b. STAND TYPE III. Frequency, mean cover and variance of tree species.

Species	Common name	Frequency	Mean Cover (%)	Variance
Abies balsamea	Balsam fir	-	-	-
Acer negundo	Manitoba maple	0.64	9.91	107.88
Betula papyrifera	Paper birch	0.13	1.22	16.41
Fraxinus pennsylvanica	Green Ash	0.90	11.26	87.27
Picea glauca	White spruce	-	-	-
Populus balsamifera	Balsam poplar	-	-	-
Populus tremuloides	Trembling aspen	0.82	22.28	280.21
Quercus macrocarpa	**Bur oak**	**1.00**	**17.55**	**183.76**
Ulmus americana	American Elm	0.28	2.35	17.54

APPENDIX 6c. STAND TYPE III. Mean basal area per 100 m^2 for each tree species in canopies 1-4.

Species	Common name		Canopy layer			
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Acer negundo	Manitoba maple	0.051	-	0.024	0.022	-
Betula papyrifera	Paper birch	0.004	-	0.003	0.001	-
Fraxinus pennsylvanica	Green ash	0.044	0.003	0.032	0.009	-
Picea glauca	White spruce	-	-	-	-	-
Populus balsamifera	Balsam poplar	-	-	-	-	-
Populus tremuloides	Trembling aspen	0.173	0.168	0.004	-	-
Quercus macrocarpa	Bur oak	0.084	0.004	0.064	0.019	-
Ulmus americana	American elm	0.018	0.006	0.011	0.001	-

APPENDIX 6d. STAND TYPE III. Mean density per 100 m^2 for each tree species in canopies 1-5.

Species	Common name		Canopy layer				
		Total	1	2	3	4	5
Abies balsamea	Balsam fir	-	-	-	-	-	-
Acer negundo	Manitoba maple	8.72	0.05	0.69	1.97	0.36	5.64
Betula papyrifera	Paper birch	0.41	-	0.08	0.18	-	0.15
Fraxinus pennsylvanica	Green ash	8.33	0.05	1.03	2.49	0.85	3.92
Picea glauca	White spruce	-	-	-	-	-	-
Populus balsamifera	Balsam poplar	-	-	-	-	-	-
Populus tremuloides	Trembling aspen	7.08	2.56	0.21	0.23	0.05	4.03
Quercus macrocarpa	Bur oak	7.41	-	1.95	1.64	0.08	3.74
Ulmus americana	American elm	1.54	0.05	0.18	0.36	0.1	0.85

APPENDIX 6e. STAND TYPE III. Frequency, mean cover and variance of common shrubs (f>5%).

Species	Common name	Frequency	Mean Cover (%)	Variance
Corylus cornuta	Beaked hazelnut	1.00	54.42	575.79
Viburnum trilobum	High bush-cranberry	0.79	6.02	56.57
Prunus virginiana	Chokecherry	0.77	4.63	32.34
Amelanchier alnifolia	Saskatoonberry	0.67	4.30	38.36
Rubus idaeus	Raspberry	0.67	0.40	0.15
Lonicera dioica	Twining honeysuckle	0.62	0.66	1.06
Ribes triste	Red currant	0.62	0.40	0.22
Symphoricarpos occidentalis	Wolfberry	0.62	0.65	1.46
Rhus radicans	Poison ivy	0.56	1.07	4.05
Acer spicatum	Mountain maple	0.51	11.30	411.60
Prunus pensylvanica	Pin cherry	0.44	1.63	7.57
Viburnum lentago	Nannyberry	0.44	4.03	60.60
Viburnum rafinesquianum	Downy arrowwood	0.41	0.93	3.38
Rosa acicularis	Prickly rose	0.36	0.66	4.57
Symphoricarpos albus	Snowberry	0.36	0.15	0.05
Cornus stolonifera	Dogwood	0.31	2.86	38.56
Diervilla lonicera	Bush-honeysuckle	0.10	0.04	0.02
Ribes oxycanthoides	Northern gooseberry	0.10	0.02	0.01

APPENDIX 6f. STAND TYPE III. Frequency, mean cover and variance of common herb species (f>5%).

Species	Common Name	Frequency	Mean Cover (%)	Variance
Aralia nudicaulis	Wild sarsaparilla	0.90	11.05	112.12
Carex peckii/pensylvanica	Carex species	0.87	2.37	12.50
Maianthemum canadense	Wild lily-of-the-valley	0.87	2.71	10.30
Oryzopsis asperifolia	Rice grass	0.77	0.49	0.18
Thalictrum venulosum	Veiny meadow-rue	0.72	0.96	0.91
Aster ciliolatus	Lindley's aster	0.69	1.70	3.06
Sanicula marilandica	Snakeroot	0.69	1.69	3.75
Pyrola asarifolia	Pink wintergreen	0.64	0.51	0.74
Fragaria virginiana	Strawberry	0.51	0.84	1.29
Anemomne quinquefolia	Wood anemone	0.49	0.39	0.31
Galium triflorum	Sweet scented bedstraw	0.46	0.36	0.31
Trillium cernuum	Nodding trillium	0.44	0.22	0.11
Galium boreale	Northern bedstraw	0.38	0.15	0.08
Smilacina stellata	Star-flowered Solomon's seal	0.36	0.83	2.83
Thalictrum dasycarpum	Tall meadow-rue	0.33	0.72	2.52
Viola species	Violet species	0.31	0.16	0.09
Matteuccia struthiopteris	Ostrich fern	0.28	3.63	64.43
Osmorhiza longistylis	Sweet cicely	0.26	0.48	1.50
Solidago canadensis	Canada goldenrod	0.26	0.33	0.51
Disporum trachycarpum	Fairybells	0.21	0.18	0.18
Lathyrus venosus	Wild peavine	0.21	0.15	0.22
Rudbeckia laciniata	Tall coneflower	0.21	0.24	0.38
Rubus pubescens	Dewberry	0.18	0.35	0.67
Lysimachia ciliata	Fringed loosestrife	0.15	0.27	0.58
Smilax herbacea	Carrionflower	0.13	0.20	0.38
Aster species	Aster species	0.10	0.10	0.09
Bromus inermus	Brome grass	0.10	0.06	0.05
Cornus canadensis	Bunchberry	0.10	0.19	0.48
Heracleum lanatum	Cow parsnip	0.10	0.21	0.54
Equisetum pratense	Marsh horsetail	0.08	0.24	1.96
Actaea rubra	Red baneberry	0.05	0.10	0.20
Aquilegia canadensis	Wild columbine	0.05	0.05	0.05
Lathyrus ochroleucus	Creamy peavine	0.05	0.03	0.02
Mertensia paniculata	Tall lungwort	0.05	0.05	0.05
Mitella nuda	Bishop's cap	0.05	0.04	0.04
Petasites sagittatus	Arrow-leaved colt's-foot	0.05	0.26	1.58
Rudbeckia serotina	Black-eyed Susan	0.05	0.16	0.67
Taraxacum officinale	Dandelion	0.05	0.02	0.01
Vicia americana	American vetch	0.05	0.01	0.00
Mosses				
Brachythecium species	Feather mosses	0.21	0.26	0.36
Mnium species	Leafy mosses	0.10	0.21	1.06

APPENDIX 6g. STAND TYPE IIIA. Relative frequency of tree species for each tree species in canopies 1-4.

Species	Common name	Canopy layer				
		Total	1	2	3	4
Abies balsamea	Balsam fir	-	-	-	-	-
Acer negundo	Manitoba maple	0.39	-	0.17	0.30	0.13
Betula papyrifera	Paper birch	0.13	-	0.04	0.13	-
Fraxinus pennsylvanica	Green ash	0.83	-	0.39	0.70	0.30
Picea glauca	White spruce	-	-	-	-	-
Populus balsamifera	Balsam poplar	-	-	-	-	-
Populus tremuloides	Trembling aspen	1.00	0.96	0.22	0.22	0.09
Quercus macrocarpa	**Bur oak**	**1.00**	-	**0.74**	**0.65**	**0.13**
Ulmus americana	American elm	0.22	0.04	0.04	0.17	0.09

APPENDIX 6h. STAND TYPE IIIB. Relative frequency of tree species for each tree species in canopies 1-4.

Species	Common name	Canopy layer				
		Total	1	2	3	4
Abies balsamifera	Balsam fir	-	-	-	-	-
Acer negundo	Manitoba maple	1.00	0.13	0.56	0.88	0.25
Betula papyrifera	Paper birch	0.13	-	0.06	0.13	-
Fraxinus pennsylvanica	Green ash	1.00	0.13	0.69	0.69	0.31
Picea glauca	White spruce	-	-	-	-	-
Populus balsamifera	Balsam poplar	-	-	-	-	-
Populus tremuloides	Trembling aspen	0.56	0.44	0.06	0.13	-
Quercus macrocarpa	**Bur oak**	**1.00**	-	**0.88**	**0.44**	-
Ulmus americana	American elm	0.38	0.06	0.31	0.19	0.06

APPENDIX 6i. STAND TYPE IIIA. Mean Density and frequency of seedlings and suckers per plot.

Species	Common Name	Seedlings		Suckers	
		Frequency	Density	Frequency	Density
Abies balsamea	Balsam fir	-	-	-	-
Acer negundo	Manitoba maple	0.43	1.09	0.26	4.70
Betula papyrifera	Paper birch	-	-	-	-
Fraxinus pennsylvanica	Green ash	0.83	3.57	0.30	1.52
Picea glauca	White spruce	-	-	-	-
Populus tremuloides	Trembling aspen	-	-	0.74	3.09
Quercus macrocarpa	**Bur oak**	**0.65**	**2.39**	**0.30**	**2.26**
Ulmus americana	Elm	0.26	0.74	0.04	0.04

APPENDIX 6j. STAND TYPE IIIB. Mean Density and frequency of seedlings and suckers per plot.

Species	Common Name	Seedlings		Suckers	
		Frequency	Density	Frequency	Density
Abies balsamea	Balsam fir	-	-	-	-
Acer negundo	Manitoba maple	0.75	3.56	0.25	1.88
Betula papyrifera	Paper birch	-	-	0.06	0.38
Fraxinus pennsylvanica	Green ash	0.69	1.63	0.13	0.63
Picea glauca	White spruce	-	-	-	-
Populus tremuloides	Trembling aspen	-	-	0.56	5.31
Quercus macrocarpa	**Bur oak**	**0.56**	**1.81**	**0.13**	**1.06**
Ulmus americana	Elm	0.19	0.38	0.13	0.56

APPENDIX 7

Photographs of Stand Types

APPENDIX 7a. Stand Type I, sub-type I.A: Stand on Gorge Creek Trail

APPENDIX 7b. Stand Type I, sub-type I.B: Stand on Gravel Pit Trail.

APPENDIX 7c. Stand Type II, sub-type II.A: Stand on Payne Trail.

APPENDIX 7d. Stand Type II, sub-type II.B: Stand on Beach Ridges Trail.

APPENDIX 7e. Stand Type III, sub-type III.A: Stand on Ochre River Trail.

APPENDIX 7f. Stand Type III, sub-type III.B: Stand on Agassiz Ski Road.

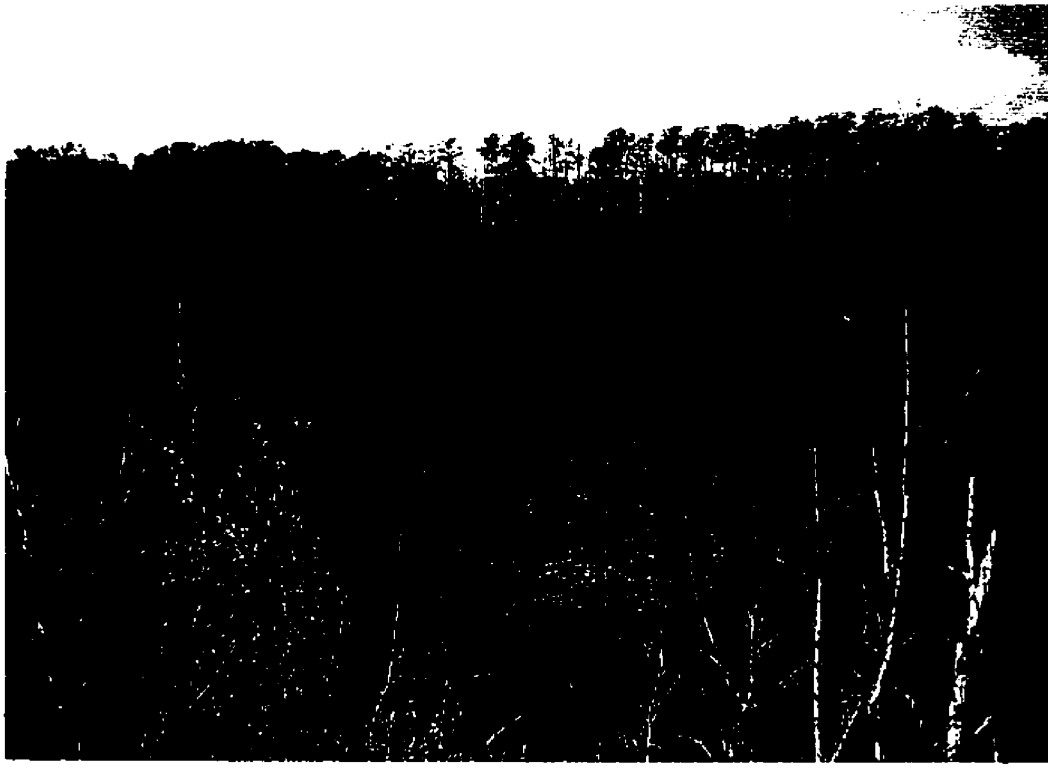
APPENDIX 7g. Stand of *Quercus macrocarpa* on a steep, south-facing slope of the Gorge Creek Trail (Stand Type I).

APPENDIX 7h. Mixed stand of *Quercus macrocarpa, Fraxinus pennsylvanica* and *Populus tremuloides* growing on mesic substrates (Stand Type III).

APPENDIX 7a. Stand Type I, sub-type I.A: Stand on Gorge Creek Trail
APPENDIX 7b. Stand Type I, sub-type I.B: Stand on Gravel Pit Trail.

APPENDIX 7c. Stand Type II, sub-type II.A: Stand on Payne Trail.
APPENDIX 7d. Stand Type II, sub-type II.B: Stand on Beach Ridges Trail.

APPENDIX 7e. Stand Type III, sub-type III.A: Stand on Ochre River Trail.
APPENDIX 7f. Stand Type III, sub-type III.B: Stand on Agassiz Ski Road.



APPENDIX 7g. Stand of *Quercus macrocarpa* on a steep, south-facing slope of the Gorge Creek Trail (Stand Type I).

APPENDIX 7h. Mixed stand of *Quercus macrocarpa, Fraxinus pennsylvanica* and *Populus tremuloides* growing on mesic substrates (Stand Type III).