Importance of Pollen Rain in Boreal Manitoba, Canada

by

Eun Ju Lee

A Thesis presented to the University of Manitoba
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy
in Botany

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

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Abstract

Importance of pollen rain as nutrient source was investigated in the boreal forest ecosystem of west-central Manitoba, Canada. Tree and tall shrub pollen rain was sampled along the 5.5 km transect in mixed boreal forest and two regenerating jack pine stands in May and June of 1991-1993 using gravity collectors. Annual pollen averaged ca. 6850 grains/cm^2 in 1992, with jack pine contributing 67.3% and spruce 24.5 % of the total. Total annual pollen deposition ranged between 16-25 kg/ha at the three sites, corresponding to nutrient inputs of 0.34-0.49 kg N/ha, 0.04-0.07 kg P/ha, and 0.11-0.20 kg K/ha. These values are small when compared to estimated rates of nutrient uptake from boreal forest. However, the combination of highly episodic, early summer deposition and very rapid nutrient turnover suggest that pollen may play an important role in supplying nutrients and promoting decomposition in the forest litter layer.

The spatial and temporal patterns of pollen infestation were investigated along a gradient of boreal microhabitats. This study shows that chytrids have roles in initial colonization and degradation of resistant pollen substrate in boreal forests and making it less refractory for other organisms. Significant differences in total pollen infestation in diverse boreal forest sites were found. The results indicated that infestation levels vary with types of decaying litter types. It is concluded that competition for nitrogen and other nutrients may occur in substrates of high C/N ratio such as in the boreal forest and chytrids adapt more favourably in dry, acidic sites with needle litters which are more hostile conditions to other decomposers. Possible linkages between pollen, chytrids, ectomycorrhizal fungi and forest tree nutrient acquisition are discussed.

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I wish to thank my supervisor, Dr. T. Booth; the members of my advisory committee, Drs. S. Badour, W.K. Kim, L. Lamari, D. Punter and M Sumner; external examiner Dr. J. Longcore; My parents, brothers and sisters.

Table of Contents

Abstract i

Acknowledgements ii

Table of Contents iii

List of Tables vii

List of Figures viii

Chapter I. General Introduction 1

The Boreal Forest 1

The Possible Role of Pollen Rain in Forest Nutrient Cycling 2

Estimate of Pollen Shed 3

Utilization of Pollen Nutrients 4

Helper Organisms 5

Mycorrhizas in Relation to Forest Nutrient Cycling 6

Linkage of Pollen, Chytrids, and Mycorrhizal Activity 6

Objectives 7

Chapter II. Pollen Deposition in the Boreal Forest of west-central Canada 8

Introduction 8

Study Area 9

Location 9

Geology and Vegetation 9

Methods 11

Study Site 11

Vegetation Sampling 12

Phenology of Pollen Deposition 12

Diural Variation in Pollen Deposition 13

Results..... 14
Daily Pollen Deposition of 1992 Season..... 14
Annual Pollen Deposition of 1991, 1992 and 1993..... 18
Diurnal Variation in Pollen Deposition..... 22
Discussion..... 22
Influence of Vegetation on Pollen Deposition..... 22
Influence of Weather on Pollen Deposition..... 25
Present and Past Pollen Deposition in Flin Flon area..... 26

Chapter III. Atmospheric Deposition of Macronutrients by Pollen in the Boreal Forest..... 28
Introduction..... 28
Methods..... 29
Study Area..... 29
Study Sites..... 31
Pollen Deposition..... 32
Jack Pine Pollen Macronutrient Analysis..... 34
Results..... 35
Pollen Depostion in the Mixed Boreal Forest..... 35
Macronutrient Concentration in Pollen..... 36
Pollen Deposition in Two Regenerating Jack Pine Stands.... 36
Water-Extractable Pollen Macronutrients..... 42
Discussion..... 42
Macronutrient Deposition by Pollen Rain..... 42
Nutritional Perspective of Pine Pollen..... 44
Distribution and Cycling of Nutrients in Jack Pine Stands.... 44
Macronutrient Fluxes by Pollen Rain to Lake Ecosystem..... 46

Chapter IV. Chytrid Distribution in Selected Boreal Manitoba Sites..... 47
Introduction..... 47
Materials and Methods..... 49
Study Area..... 49
Soil Collection and Laboratory Observation..... 51
Similarity of Chytrid Assemblages between Sites..... 52
Results..... 52
Litter Types..... 52
Pollen Infestation by Site..... 54
Chytrid Diversity and Distribution..... 54
Chytrid Dominance..... 56
Coefficients of Association..... 56
Species in Common..... 59
Discussion..... 59
Pollen Infestation by Site..... 60
Species Diversity..... 61
Chytrid Distribution and Dominance..... 61
Species Assemblages and Litter Types..... 63

Chapter V. Factors Affecting Pollen Infestation by Chytrids
in Boreal Manitoba..... 65
Introduction..... 65
Materials and Methods..... 67
Study Area..... 67
Study Area Climate..... 69
Woody Vegetation, Dominance and Openess..... 69
Soil Analysis..... 71

Pollen Deposition 71
Chytrid Sampling and Data Processing 72
Results 73
Site Characteristics 73
Spatial Considerations: Pollen Infestations and Environmental Factors 76
Temporal Considerations: Litter Types and Pollen Infestation 82
Temporal Considerations: Pollen Infestations by Selected Species in Litter types 82
Discussion 87

Chapter VI. General Discussion 93
Deposition of Macronutrients by Pollen 93
Pollen and Environmental Specificity 95
Colonization Strategies and Interactions 96
Future Research 97

Literature cited 99
Appendix I. Site Descriptions of 88 Sites 111
Appendix II. Vegetation Data 115
Appendix III. Pollen Data 120
Appendix IV. Soil Data of 88 sites 134
Appendix V. Chytrid Infestation data 136
Appendix VI. Chytrid Species Descriptions 143
Appendix VII. Temporal Distribution of Ectomycorrhizal Fungi 152
Appendix VIII *Suillus brevipes* Hyphal Growth Experiment 156

List of Tables

Table 2.1	Composition of mixed boreal forest at study area	15
Table 2.2	Total tree and tall shrub pollen deposition	16
Table 2.3	Weather conditions for May and June 1991-1993	20
Table 3.1	Forest composition in the two 25-year old regenerating jack pine stands	33
Table 3.2	Tree pollen deposition for 1991-1993	37
Table 3.3	Macronutrient concentrations in jack pine pollen	38
Table 3.4	Annual macronutrient deposition by jack pine pollen	39
Table 3.5	Annual macronutrient deposition by spruce, alder and willow pollen	40
Table 3.6	Macronutrient deposition by jack pine pollen in the two 25-year old regenerating jack pine stands	41
Table 3.7	Water-extractable macronutrients in jack pine pollen	43
Table 4.1	Site designations and descriptions of the selected 13 sites	53
Table 4.2	Pollen infestations in selected boreal Manitoba sites	55
Table 4.3	Pollen infestations by chytrid species from the selected sites in boreal Manitoba	57
Table 5.1	Site designations and soil collection descriptions	74
Table 5.2	Pearson product-moment correlation coefficient of environmental factors and pollen infestation	78
Table 5.3	Epibiotic chytrid infestation of jack pine pollen along a gradient of microhabitats in boreal Manitoba	79

List of Figures

Figure 2.1	Location of the studt area and a 5.5-km transect	10
Figure 2.2	Pollen deposition in 1992	17
Figure 2.3	Jack pine pollen deposition in 1991, 1992 and 1993	19
Figure 2.4	Spruce pollen deposition in 1992 and 1993	21
Figure 2.5	Diurnal deposition of jack pine pollen	23
Figure 3.1	Location of the study area in west-central Manitoba	30
Figure 4.1	Locations of 13 selected boreal Manitoba sites	50
Figure 4.2	Coefficients of association for fungal assemblages in site parings	58
Figure 4.3	Chytrid species in common among site parings	60
Figure 5.1	Location of the study area (Mistik Creek) in Manitoba	68
Figure 5.2	Weather conditions for Apr.-Nov., 1992 and Apr.-Oct., 1993	70
Figure 5.3	Relationship between types of litter-soil and moisture levels	77
Figure 5.4	Relationship between litter-soil types and pollen infestation	81
Figure 5.5	Plots of pollen infestation and individual chytrid occurrences correlated with soil pH	83
Figure 5.6	Pollen infestations on seven sampling dates from three different litter types	84
Figure 5.7	Infestation percentages on seven sampling dates of four chytrid species in three different litter types	86

Chapter I
General Introduction

The Boreal Forest

The boreal forest, or taiga, is a broad, circumpolar mixture of cool coniferous and deciduous tree species which covers over 14.7 million km^2, or 11%, of the earth's terrestrial surface (Bonan and Shugart 1989). The boreal forest forms a circumpolar belt about the Northern Hemisphere. In Eurasia it begins in Scandinavia and extends across the continent to northern Japan. In North America the boreal forest extends from Labrador across Canada and through Alaska to the Brooks Range. It is dominated by four genera of conifers, *Picea*, *Abies*, *Pinus*, and *Larix*, and two genera of deciduous trees, *Populus* and *Betula*. Dominant species include black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). Occupying, for the most part, glaciated land, the boreal forest is also a region of upland granite ridges, alder thickets, bogs, rivers, and cold lakes.

In Manitoba, located in central Canada, the boreal forest extends from Lake of the Woods in the southeastern corner of the province to Reindeer Lake, which is well towards the northwest. Much of this area is underlain by Precambrian rock formations with a comparatively thin soil mantle. The boreal forest also covers part of the area where the parent material is limestone, especially along part of the west shore of Lake Winnipeg, around the northern part of Lake Winnipegosis and both north and south of The Pas marshes.

Major vegetative components include, white spruce (*Picea glauca* [Moench] Voss), on well drained but not excessively drained sites, and black spruce (*Picea mariana* [Mill.] BSP), on poorly drained and wet sites. Stands of jack pine (*Pinus banksiana* Lamb.) are common on upland sites after fire, particularly on such dry substrata as sand plains and eskers. Much of the region has been influenced by forest fires and secondary communities of trees and shrubs are common. After fire these stands may be replaced by a young forest of black spruce, jack pine or aspen, depending on the available seed. Alluvial soils often bear good stands of white spruce, balsam poplar and balsam fir. Peat-filled depressions are occupied by black spruce muskeg, a continuous forest of poorly grown trees, with a dense floor of ericaceous shrubs and sphagnum or other mosses. Wetter peat deposits are covered by treeless bog in which sedge species (*Carex*) are conspicuous (Weir 1960). Black spruce and jack pine account for 30.9 % and 21.6 % respectively of Manitoba's forest lands (Anonymous 1985).

The Possible Role of Pollen Rain in Forest Nutrient Cycling

Among the types of fine organic matter, such as insect frass, spores and pollen, available in forest ecosystems, pollen is overlooked in many nutrient cycling studies in spite of significantly high concentrations of nutrients such as 2% nitrogen in dry weight (Grier et al. 1974). Foster and Morrison (1976) did not consider pollen in their model of nutrient dynamics in boreal jack pine forests, despite the fact that jack pine produces considerable quantities of pollen annually.

Few studies provide insights into the role of pollen in forest nutrient cycling. Stark (1972) suggested that nutrients found in pollen allow fungi to obtain sufficient energy to complete litter decay, which in turn releases other nutrients

needed for tree growth. Stark specifically reported that pollen was primarily infested by hyphal fungi, not by members of the Chytridiales (commonly referred to as zoosporic fungi) even though these organisms are known to degrade pollen. Recent studies (Hutchison and Barron 1997) showed that many lignicolous fungi are capable of degrading pollen.

Doskey and Ugoagwu (1989) determined that pine pollen is an important source of macronutrients to oligotrophic lakes in northern Wisconsin. Also Hutchison (pers. comm.) suggests that early stage ectomycorrizal fungi attack and derive nutrients from pollen.

Estimate of Pollen Shed

The rain of pollen commonly occurring in temperate and boreal forests can deliver notable quantities of nutrients. For example, Stark (1972) reported that from 0.9 to 3 kg/ha/yr of pollen rain fell in a stand of Jeffrey pine in Nevada, supplying 38g nitrogen, 15g potassium, 8.5g phosphorus, 8.3g magnesium, and 0.56g calcium. Although this level of nutrient input appears to be too low to account for the total seasonal growth of trees, nitrogen, phosphorus and other elements in pollen can be essential to the activities of fungal and other types of organisms (Stark 1972; Price et al. 1989). Furthermore, during summer when minimal amounts of nitrogen and phosphorus are leached from the fermentation layer, pollen is the main nutrient source for fungi (Stark 1972). In northern Wisconsin, 3.5kg - 80.0 kg/ha pollen deposition was estimated for white and red pine (*Pinus strobus* L., *P. resinosa* Ait.) stands (Doskey and Ugoagwu 1989).

In this study area in west-central Manitoba, sphagnum bogs are prevalent and these bogs are known to be optimal habitats for chytriaceous fungi in other areas

(Lange 1978). The soils and peat of the study area are acidic suggesting that chytrids may play a major role in pollen degradation unlike the situation in the more alkaline soils of the previously reported Nevada study. Pollen may play a direct role in providing soluble nutrients to forest trees, or it provide the nutrients via a series of intermediaries including chytrids and mycorrhizas. Chytrid activity may release nutrients that stimulate mycorrhizal fungi and other fungi, which in turn provide nutrients to trees.

Utilization of Pollen Nutrients

While bees are the principal consumers of pollen, beetles, flies larvae, and spring-tails also ingest pollen (Stanley and Linskens 1974). Bees, beetles, and most other insects excrete the exine after consuming the pollen protoplasm because they lack the capacity to degrade sporopollenin.

For over a hundred years pollen has been used as bait for zoosporic aquatic fungi. Chytrids (Chytridiomycota) have existed on our planet for an extremely long time (Taylor et al. 1992). Aquatic fungi infesting pollen were first reported with the publication of Braun's (1855) studies on *Rhizophydium pollinis-pini* (Braun) Zopf. Since then, numerous investigators (Sparrow 1960) have observed that chytrids break down pollen in nature. Chytrids also degrade such resistant compounds as cellulose, chitin, and keratin (Whiffen 1941; Ajello 1948; Karling 1947).

Goldstein (1960) surveyed the effect of zoosporic fungi (including chytrids) on 31 species of angiosperm and gymnosperm pollen grains and reported on the differential susceptibility of the various types of pollen to fungal attack. Skvarla and Anderegg (1972) illustrated that the protoplast and intine of cedar pollen

appeared to be excavated by the chytrid *Rhizophidium* sp.. As previously stated, zoosporic fungi (including chytrids) are commonly encountered on naturally occurring substances such as pollen and other forms of cellulosic litter. The ability of chytrids to infest pollen may reflect their chemotactic abilities. Zoospores of some Chytridiomycete species encyst preferentially on suitable substrates (Mitchell and Decon 1986).

Helper Organisms

On observation of interactions between rhizosphere microflora and ectomycorrhizal fungi, it has been suggested that some microorganisms play a role in the establishment of the mycorrhizal symbiosis (Bowen and Theodorou 1979; Garbaye and Bowen 1989). Some organic substances present in the plant rhizosphere, such as amino acids, plant hormones, and vitamins, may be produced by soil microorganisms and may enhance the development of mycorrhizal fungi in the absence of any host plant.

Thus, helper organisms (*sensu stricto*) are microorganisms located inside the mantle that act as 'helpers' to stimulate mycelial growth of mycorrhizal fungi or to promote mycorrhiza formation (Garbaye and Bowen 1989). *Sensu lato*, helper organisms degrade litter, including pollen, and directly or indirectly, via mycorrhizal fungi, provide nutrients to phytobionts (plant components of the mycorrhizal symbiosis). In my study helper organisms include: photosynthetic and non-photosynthetic monerans, filamentous and non-filamentous fungi, protista, algae, microfauna and macrofauna.

Mycorrhizas in Relation to Forest Nutrient Cycling

The widespread occurrence of mycorrhizas in nature and their importance in the mineral nutrition of almost all plants has been extensively documented (e.g. Donald and Carroll 1981). Fogel's study (1980) indicates that mycorrhizas account for 50% of the annual throughput of biomass and for 43% of the nitrogen released annually in a Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) ecosystem. The enhancement of ion uptake particularly of phosphorus and its translocation by mycorrhizal fungi is well known (Bowen 1973). Direct nutrient recycling, through mycobionts capable of decomposing leaf and other litter materials, is also well documented (Went and Stark 1968). Cromack et al. (1975) reported that samples of forest basidiocarps and rhizomorphs had significantly greater concentrations of potassium, sodium, phosphorus, calcium, and zinc than forest floor leaf litter, further establishing the importance of these fungi as nutrient sinks in the ecosystem.

Linkage of Pollen, Chytrids, and Mycorrhizal Activity

Pollen, which lands on the soil litter surface in June, moves by wind, water, or gravity into the fermentation zone during July and August where it is infested by filamentous fungi (Stark 1972). In my study, it is assumed that initial infestation by chytrids occurs at the litter surface and continues as transport into the fermentation zone takes place. The number of ectomycorrhizal root tips increases during June and July in Douglas fir / Larch forest soil in Western Montana (Harvey et al. 1990). Widden and Parkinson (1973) also observed a peak in mycelial content during August in soils of *Pinus strobus* L. forests in Ontario. This increase may be due, in part, to an increase of the mycelia of mycorrhizal fungi. I hypothesize that previous to and during this period nutrients brought in

by pollen play a critical role in supporting the activities of mycorrhizal fungi and other microorganisms.

Objectives

This series of studies was designed to increase the understanding of environmental and mycological aspects of pollen rain in the boreal forest in Manitoba. In contrast to the wealth of information on other litter types, little is known of the importance of pollen as nutrient source in the boreal forest nutrient cycling. The general objective of this study was to determine the importance of pollen rain in the boreal forest nutrient cycling in west-central Manitoba. More specifically, the objectives were: (i) to measure the spatial and temporal variation in pollen deposition and relate it to floristic variation and meteorological conditions; (ii) to determine the macronutrient content of pollen, and determine the contribution of pollen to atmospheric deposition of macronutrients in boreal Manitoba; (iii) to determine the distribution of pollen decomposing chytrids in soils from diverse boreal Manitoba sites; (iv) to determine the abiotic and biotic factors that affect infestation of pollen ; (v) to determine seasonal patterns of pollen infestation in soils of different types and containing different kinds of litter; and (vi) discuss possible linkages between pollen, chytrids, ectomycorrhizal fungi and acquisition of nutrients by trees in boreal Manitoba.

In summary, my objective is to understand pollen as a nutrient source in boreal forests and to indicate the importance of chytrids, and their interactions in nature.

Chapter II
Pollen Deposition in the Boreal Forest of West-Central Canada

INTRODUCTION

In many temperate forest ecosystems, large quantities of tree pollen are deposited over a short period in early summer (Doskey and Ugoagwu 1989). Because pollen grains decompose rapidly and have high macronutrient concentrations, the pollen rain may be an important component of nutrient dynamics in natural terrestrial and aquatic ecosystems (Stark 1972; Doskey and Ugoagwu 1989). Despite this, pollen has been overlooked in studies of boreal forest nutrient cycling (e.g. Foster and Morrison 1976).

Pollen deposition studies in anthropogenically-altered regions of continental North America have quantified human allergens (e.g. Walton and Dudley 1947; Durham 1933; Bassett 1964). Lichti-Federovich and Ritchie (1964) examined contemporary atmospheric and sediment pollen rain along the forest-grassland transition in southern Manitoba. However, little information is available on the phenology of pollen deposition in the natural boreal forests of continental North America.

A number of studies have described late-Wisconsinan pollen stratigraphy in the western interior of Canada (summarized in Ritchie 1976, 1987; Ritchie and Yarranton 1978; MacDonald and Ritchie 1986). In these studies, pollen assemblages preserved in lake sediments and peat were used to reconstruct past vegetation. However, interspecific differences in pollen production, dispersion,

deposition, and preservation limit the resolving power of paleo-vegetation reconstructions (Erdtman 1943; Prentice 1985). Information on pollen deposition in natural boreal forest stands would be useful in helping refine interpretations of the fossil pollen record.

This study was designed to examine early summer (1991-1993) deposition of pollen in boreal mixed-forest stands in west-central Manitoba, Canada. The objectives were to determine pollen deposition and temporal profiles for dominant tree and tall shrub species, to examine inter-annual variation in spruce and jack pine pollen deposition, and to quantify diurnal variation in the deposition of jack pine pollen.

STUDY AREA

Location

The study area is located in west-central Manitoba (54°40'N, 101°30'W), approximately 10 km north-west of Cranberry Portage (Fig. 2.1). Mean elevation is approximately 300 m a.s.l. The climate is sub-humid continental, with mean annual precipitation of 484 mm and a mean annual temperature of -0.5°C. Prevailing winds are from the north-west. Climate data is based on 27 year normals (1964-1990) at Flin Flon airport weather station, approximately 11 km north-west of the study area.

Geology and Vegetation

The study area lies on the Canadian Precambrian Shield. Intense glaciation has resulted in irregular relief characterized by granitic rocky ridges separating poorly drained depressions and narrow lakes. Exposed rock barrens are common,

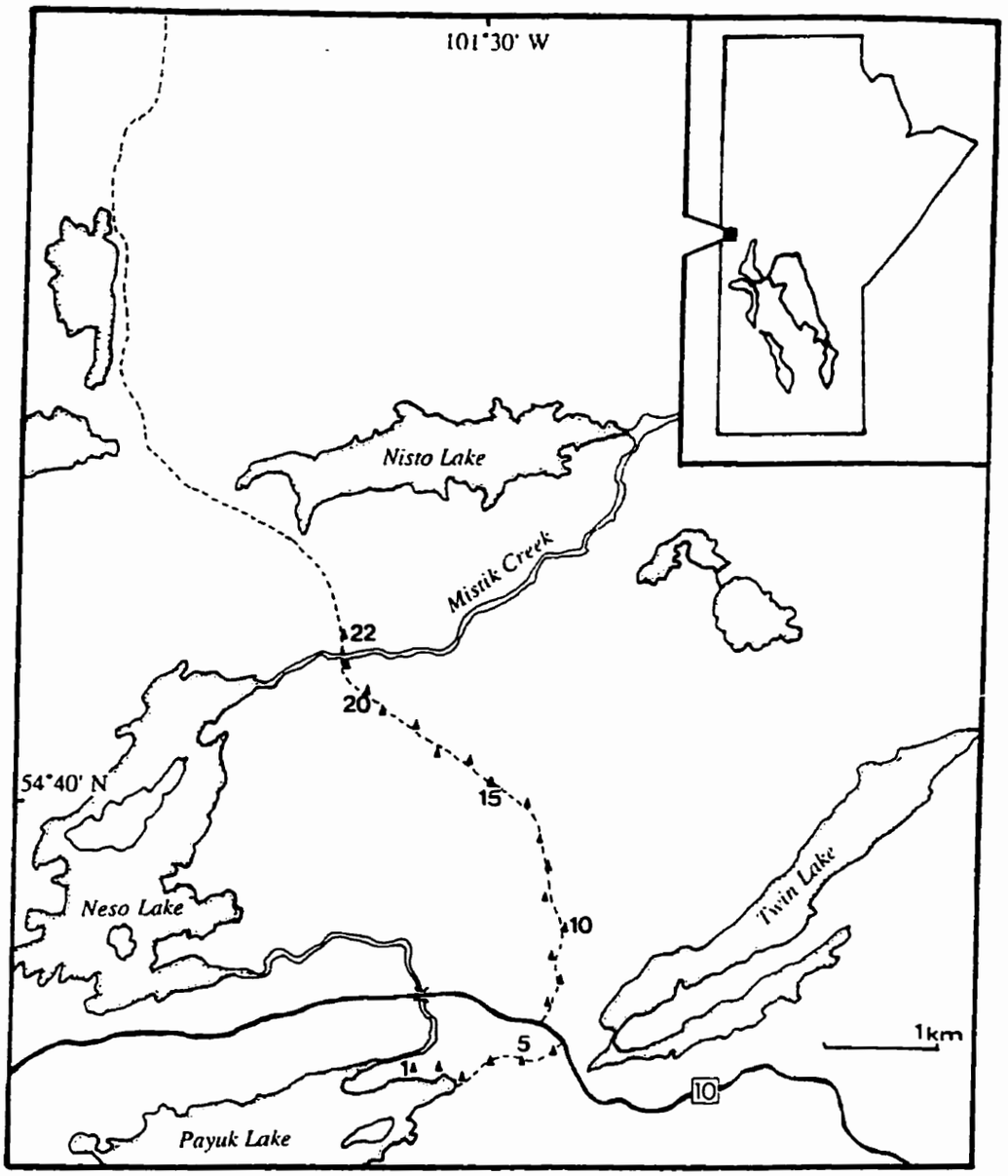

Fig. 2.1. Location of the study area in west-central Manitoba, Canada. The 5.5 km transect is located along the Sherridon Road (dotted line). The 22 sampling station locations are indicated by triangles.

and soils are generally thin and of low fertility with a weakly developed podzolic profile (Rowe 1972).

The region lies within the northern coniferous section of the boreal forest (Rowe 1972). Black spruce (*Picea mariana* [Mill.] BSP.) is the dominant tree of poorly drained lowlands. Jack pine (*Pinus banksiana* Lamb.) is common on well-drained sands and on the thin soils of upland rock outcrops. Under more favourable soil conditions, white spruce (*Picea glauca* [Moench] Voss), balsam fir (*Abies balsamea* [L.] Mill.), aspen poplar (*Populus tremuloides* Michx.) and balsam poplar (*P. balsamifera* L.) form mixed stands. The study transect is located in a mixed boreal forest stand of density ca. 3200 trees/ha. Trees are 8-30 m high with a mean diameter of 11.2 cm at breast height. Mean age of jack pine trees in the area is 65 yrs (n = 49).

METHODS

Study Site

A 5.5 km transect through mature boreal mixed-forest was established along the Sherridon road between Payuk Lake and Mistik Creek (Fig. 2.1). This region is readily accessible, and is representative of the boreal forests of west-central Canada. Twenty-two sampling stations (regularly spaced, ≈ 250 m apart) were established along the transect for sampling in 1992 and 1993. At each sampling station, two pairs of pollen collectors were established, one pair on each side of the road (88 pollen collectors in total, detailed site descriptions in Appendix I). Collector pairs were located at least 10 m apart. To minimize forest-road edge

effects, collectors were randomly located between 12 and 44 m from the road. In 1991, twenty-six pollen collectors at 13 sampling stations were sampled.

Vegetation Sampling

Information on forest stand along the transect was determined using the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). At each sampling station, two transects (one on each side of the road) were located from the roadside into the forest. Ten points were located at 10 m intervals along each transect, and at each point the distance to and basal area of the nearest tree (> 2.5 cm in diameter and > 2m in height) in each of four quadrants were measured. A total of 1760 trees and tall shrubs were counted and measured.

Phenology of Pollen Deposition

In 1991, pollen sampling was undertaken from May 31-June 17 to determine deposition of jack pine pollen. The sampling period was extended in 1992 (May 3-June 22) to allow for measurement of pollen deposition by all tree and tall shrub species in the region. In 1993, sampling occurred from May 20 - June 18 to determine deposition of jack pine and spruce pollen. In 1992, collected catkins and male cones were observed daily to determine timing of pollen release. Flowering periods for each species were subjectively determined to include the time during which at least 10% of cones or flowers were undergoing anthesis. A similar approach was used by Ritchie (1977).

Durham (1946) gravity pollen collectors were used in this study. These collectors were selected in preference to mechanical samplers for reasons of: i) cost; ii) inaccessibility to power for mechanical samplers; iii) the likelihood of

animal damage; and iv) the need for uninterrupted data collection. A Durham pollen collector consists of two horizontal disks (23 cm in diameter, 15 cm apart), with the lower disk 9 cm from ground level. A standard 2 x 8 cm glass slide covered with a thin film of petroleum jelly was placed on the lower disk to collect pollen. Slides were exposed for 24 hours (1991) or 48 hours (1992, 1993). Slides were kept in a tightly sealed slide box before and following exposure to prevent contamination, and were examined within 24 hours under a stereo-microscope (100x magnification) to identify and estimate amounts of pollen. Reference slides were used to aid in pollen identification: spruce, alder and willow pollen could only be identified to genus. Pollen deposition was determined by counting all grains within a randomly selected 0.18 cm^2 area. Amounts of pollen rain were expressed as the number of pollen grains/cm^2. Raw data, and voucher slides from the 1992 field station, are available from Dr. Tom Booth, Department of Botany, University of Manitoba.

Diurnal Variation in Pollen Deposition

Diurnal variation in jack pine pollen deposition was examined over a 48-hour period from June 7-8, 1993. The experiment, which was carried out at sampling station 3 near Payuk Lake (Fig. 2.1), consisted of exposing slides (n = 4) to catch pollen. Slides were changed every 3 hours, and stored and analyzed as described above. Microclimatic data were also measured every 3 hours during the sampling period. Wind speed was measured with an anemometer, relative humidity using a sling psychrometer, and temperature using an alcohol thermometer.

RESULTS

Daily Pollen Deposition of 1992 Season

Tree frequencies and basal area values along the 5.5 km transect are summarized in Table 2.1 (detailed vegetation data in Appendix II). The most common tree species are black spruce, trembling aspen and jack pine. Green alder (*Alnus crispa*) is the most common tall shrub.

Total pollen deposition at the 88 pollen trap sites ranged between 4,314 and 11,575 grains/cm^2 during May-June 1992. Seven tree and tall shrub pollen 'types' were identified (Table 2.2). Jack pine accounted for over two-thirds and spruce (mainly black spruce) an additional one-quarter of the total. The remaining tree and tall shrub species accounted for only minimal amounts of pollen. Pollen or spores from other species (e.g. members of the Rosaceae family, the genus *Equisetum*) were collected in very small amounts and are not summarized (detailed pollen data are listed in Appendix III).

In 1992, pollen deposition began in early May. Overall rates of deposition were relatively low prior to June 7 and pollen rain ceased after June 20. Pollen deposition of flowering plants (poplar, willow, birch, and alder) generally occurred between late April and early June (Fig. 2.2). *Alnus rugosa* released pollen in early May, and *Alnus crispa* in late May to early June. Alder pollen was unevenly distributed among sites. The pollen of birch (*Betula papyrifera* Marsh.) was fairly evenly deposited at all sites, but never in large amounts. Birch pollen rain lasted for about two weeks (May 18-May 30). Willow (*Salix* spp.) pollen was collected in small amounts throughout the sampling period, though variation among the 88 sites was high. Between May 5-30 there were two or three indistinct peaks in willow pollen deposition, probably reflecting different willow

Table 2.1. Composition of mixed boreal forest near Cranberry Portage, Manitoba (based on n = 1760 trees).

Species	Proportion of Individuals (%)	Total Basal Area (cm^2/ha)	Relative Basal Area (%)
Alnus crispa	12.2	4407	1.5
Alnus rugosa	4.2	2064	0.7
Betula papyrifera	3.9	6138	2.1
Abies balsamea	2.0	3155	1.1
Populus basamifera	2.6	9570	3.3
Populus tremuloides	10.0	50688	17.4
Larix laricina	2.0	3610	1.2
Salix spp.	5.4	1972	0.7
Picea mariana	45.3	90707	31.2
Picea glauca	4.1	67570	23.2
Pinus banksiana	8.4	51245	17.6

Table 2.2. Total tree and tall shrub pollen deposition near Cranberry Portage, Manitoba in 1992 (based on n = 88 pollen collectors). Pollen deposition values are mean ± S.D., with the range indicated in brackets.

Tree species	Total pollen deposition (grains/cm^2)	% of total	CV (%)*
Pinus banksiana	4604 ± 1316 (2595 - 7599)	67.3	28.58
Picea mariana, *Picea glauca*	1673 ± 375 (1064 - 3031)	24.5	22.41
Alnus crispa, *Alnus rugosa*	295 ± 506 (12 - 2666)	4.3	171.53
Populus tremuloides, *Populus balsamifera*	128 ± 71 (7 - 414)	1.9	55.47
Betula papyrifera	71 ± 25 (23 - 146)	1.0	35.21
Larix laricina	58 ± 43 (0 - 203)	0.8	74.14
Salix spp.	14 ± 18 (0 - 91)	0.2	128.57

* Coefficent of variation.

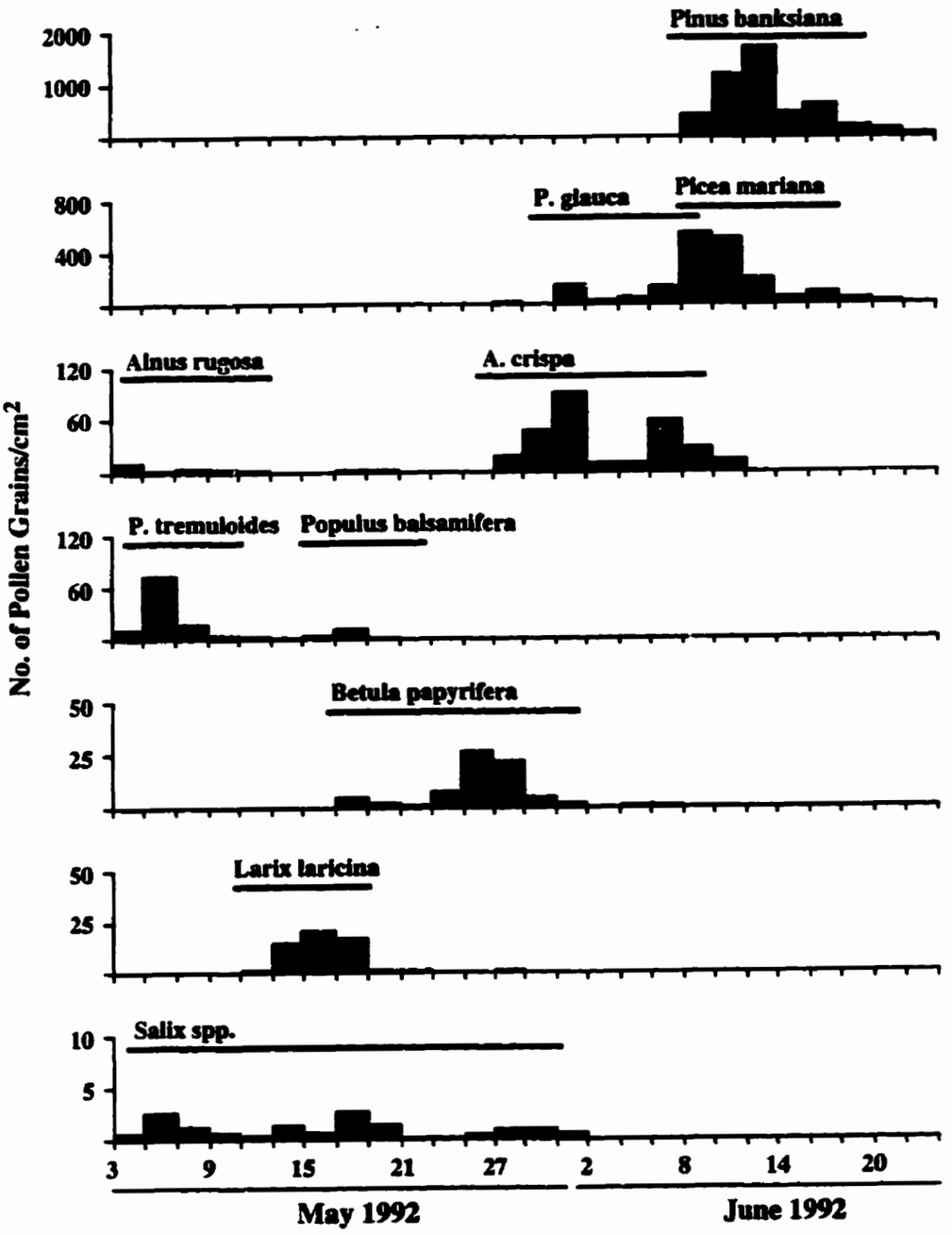

Fig. 2.2. Pollen grain deposition in 1992. Values are totals for each 48-hour period. Lines above the histograms indicate observed times of pollen release.

species. *Populus tremuloides* released pollen in early May, and *P. balsamifera* in mid-May. Poplar pollen was relatively evenly distributed among the sites.

Conifer pollen was generally released later than that of flowering plants. The exception was larch (*Larix laricina* [Du Roi] K. Koch), which deposited most of its pollen in mid-May. Larch pollen was deposited in small amounts at most sites. White and black spruce differed in the timing of pollen release, with white spruce beginning pollen release in early June, a week earlier than black spruce. Spruce pollen was fairly evenly deposited over all sites, with black spruce pollen accounting for > 80% of the total. Jack pine was the last species to release pollen, the first collection being made on June 7.

Annual Pollen Deposition of 1991, 1992 and 1993

Total jack pine pollen deposition was similar over the three sampling years: 4476 grains/cm^2 in 1991, 4604 grains/cm^2 in 1992, and 3980 grains/cm^2 in 1993. Peak periods of deposition occurred on June 3, June 12-13 and June 7-8 respectively (Fig. 2.3). Warmer than normal spring temperatures in 1991 resulted in early deposition, whereas below-seasonal temperatures in 1992 delayed deposition (Table 2.3). Release of jack pine pollen in 1992 did not occur until June 6-10, during which time the maximum daily temperature rose from 11°C to 31°C. Deposition of spruce pollen varied between years, with mean annual deposition in 1992 of 1673 grains/cm^2 but only 1060 grains/cm^2 in 1993 (Fig. 2.4). Peak periods were June 8-9, 1992 and June 3-4, 1993.

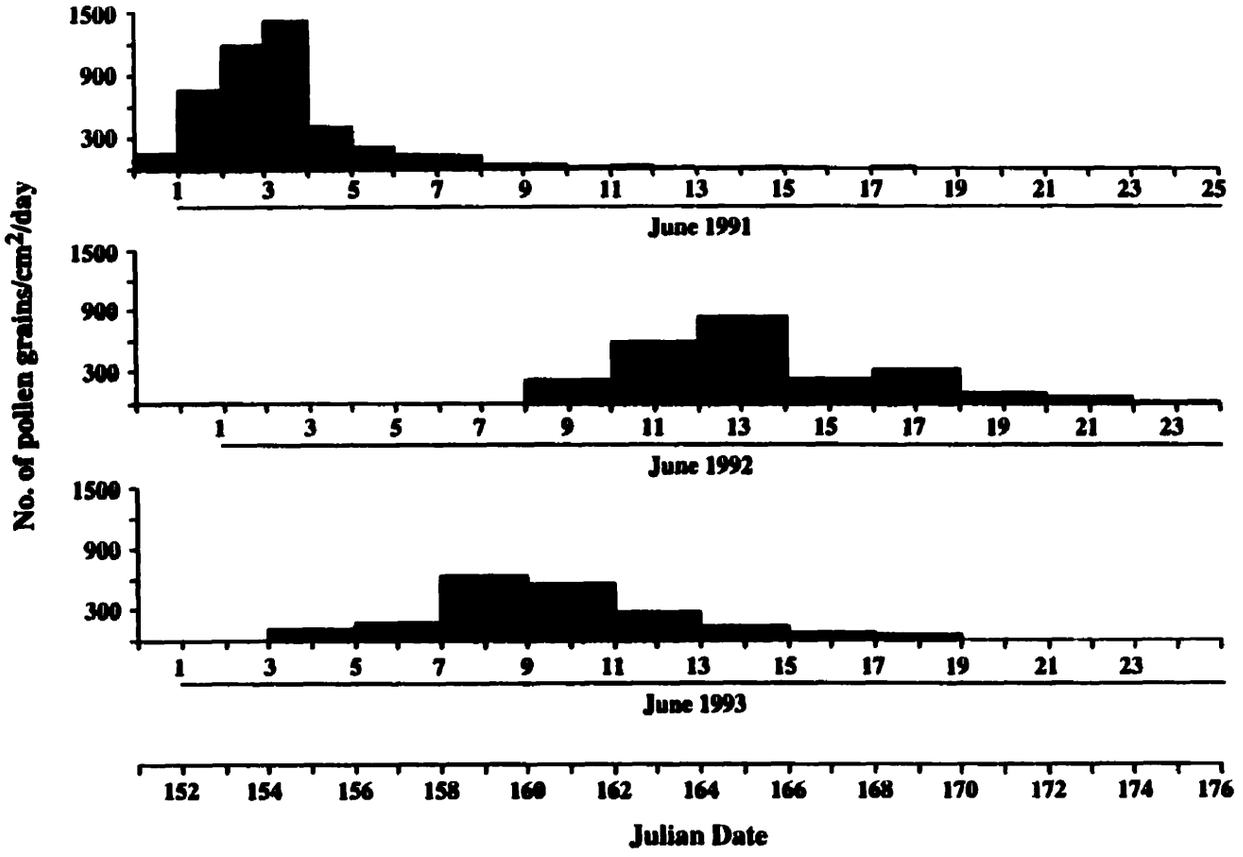

Fig. 2.3. Jack pine pollen deposition (grains/cm^2/day) in 1991, 1992 and 1993, standardized by Julian date. Note that collections were made every 24 hours in 1991, and every 48 hours in 1992 and 1993.

Table 2.3. Mean monthly temperature, precipitation, and growing degree-days (temperature > 5°C) for May and June 1991-1993 at Flin Flon Airport , and corresponding normals for the 27-year period 1964-1990.

Month	Variable	1991	1992	1993	Normals
May	Temp.(°C)	9.8	7.3	8.7	8.9
	Precip.(mm)	39.0	43.0	16.2	41.0
	Temp.>5°C	170.4	101.7	122.1	140.2
June	Temp.(°C)	16.4	12.3	13.3	14.7
	Precip.(mm)	51.6	48.8	109.2	70.2
	Temp.>5°C	341.3	222.4	246.9	291.0

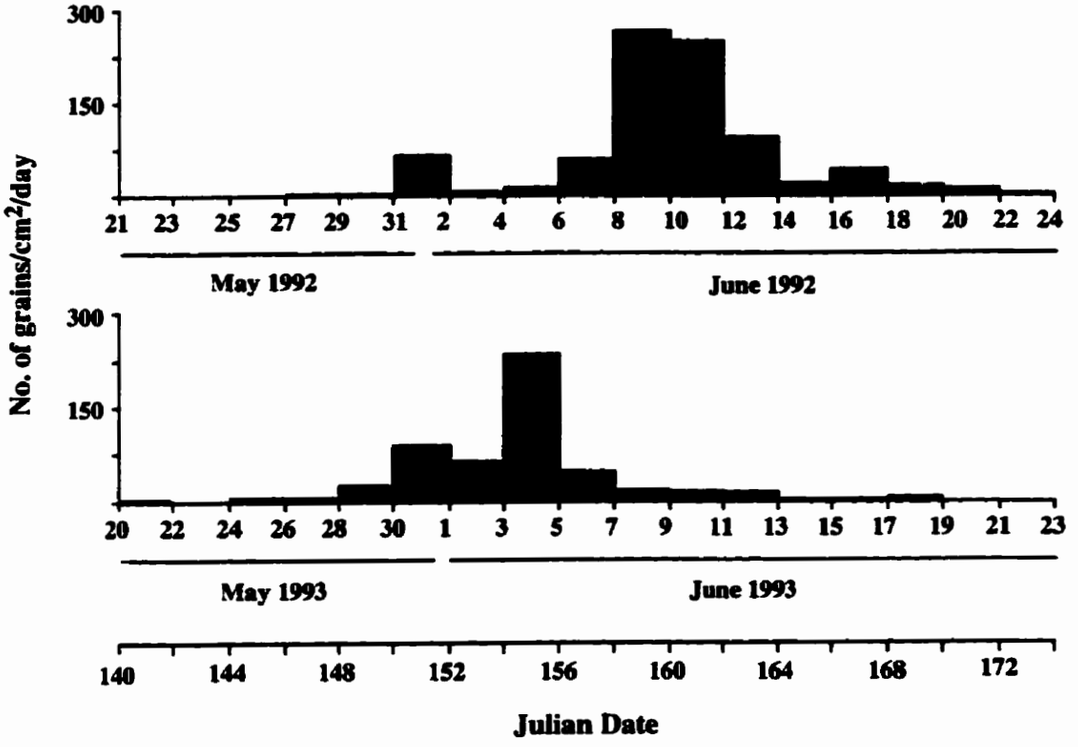

Fig. 2.4. Spruce pollen deposition (grains/cm^2/day) in 1992 and 1993, standardized by Julian date.

Diurnal Variation in Pollen Deposition

Large quantities of jack pine pollen were liberated over about 10-14 days, with peak diurnal deposition occurring during daylight hours (Fig. 2.5). Deposition was positively correlated with air temperature (r = 0.95) and windspeed (r = 0.86), and negatively correlated with relative humidity (r = -0.93). Very little pollen was deposited in the early morning (0300-0600 hours). I also noted that pollen deposition was low during cool, wet weather. These results suggest that jack pine anthesis occurs during daylight hours, though climatic conditions also play a role.

DISCUSSION

Influence of Vegetation on Pollen Deposition

Mean annual tree and tall shrub pollen deposition in the study area was ca. 6850 grains/cm^2 in 1992. This is somewhat higher than the ca. 5000 grains/cm^2 obtained by McLennan and Mathewes (1984) in coastal British Columbia.

Jack pine was disproportionately represented in our samples, accounting for 67.3% of pollen rain despite it being a relatively minor component of the forest (relative basal area = 17.6%). This result indicates that jack pine produces pollen in great quantity. Previous studies have shown that pines (genus *Pinus*) produce large amounts of pollen compared to other tree species (Stark 1972; Bradshaw and Webb 1985; Doskey and Ugoagwu 1989).

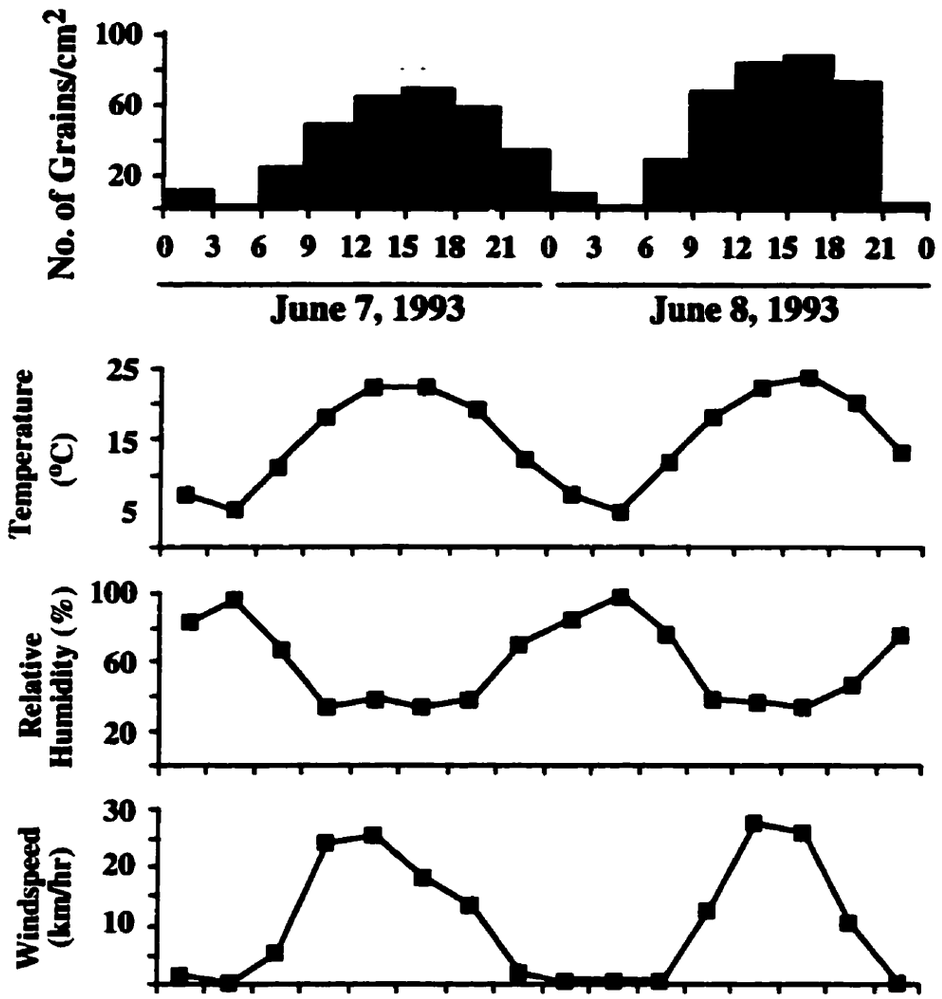

Fig. 2.5. Diurnal deposition of jack pine pollen, June 7-8, 1993 at sampling station 3. Values are totals for each 3-hour period. Temperature, relative humidity and wind speed profiles are also shown.

Spruce pollen was also well represented in the pollen spectra, accounting for 24.5% of total deposition. However, this value is low relative to the abundance of white and black spruce in these forests (relative basal area = 54.4%).

Pollen of flowering plant species (alders, poplars, willows and birch) was poorly represented. Although aspen poplar was as common as jack pine, it accounted for < 2% of total pollen deposition. Studies based on pollen deposition in lake sediments (e.g. Davis and Goodlett 1960; Webb 1974) have also revealed that aspen poplar is poorly represented in the pollen spectrum.

Interspecific differences in deposition variability along the transect are apparent (CV values, Table 2.2). Variability in jack pine and spruce were comparatively low, reflecting the relatively even spatial distribution of these species along the transect. In addition, these species generally produce microstrobili in the upper canopy branches, thus promoting long-distance wind dispersal (Bradshaw and Webb 1985). Scots pine (*Pinus sylvestris*) pollen is normally deposited within 700 m of source (Stanley and Linskens 1974), while Buell (1947) found that pine pollen deposition at 400 m was 10% of that at source. For common species, pollen dispersal may be sufficient to mask patchiness in the spatial distribution of source trees (Li and Yao 1991). Spatial variability in pollen deposition was somewhat higher in birch, poplar and larch, which probably reflects the much smaller amounts of pollen produced by these species. Variability in deposition was highest for tall shrubs (willows and alders). This likely reflects the smaller stature of these species, their patchy distribution in the field, and the low dispersability of alder pollen (Bradshaw 1981).

Influence of Weather on Pollen Deposition

Tree and tall shrub pollen deposition occurred between early May and late June of 1992. In general, pollen deposition of a given species lasted for about two weeks, with pollen release occurring earlier in flowering plants than in spruce or jack pine. Pollen release in jack pine varied between years, reflecting differences in ambient air temperatures in May and early June. Previous studies have found that the timing and extent of pollen release is strongly dependent on ambient air temperature (e.g. Bringfelt et al. 1982). In longleaf pine, low temperatures delay and extend the period of pollen release (Boyer 1973). Temperature and precipitation in early summer affected jack pine reproductive success at the northern limit of its distribution (Houle and Filion 1993).

High yields of tree pollen often occur in years following a warm, dry summer (Hyde 1952; Richie 1977). My observation of higher amounts of spruce pollen in 1992 than 1993 is consistent with this finding. Total growing degree-days (temperature > 5°C) from May - July 1991 were ca. 940, compared to only ca. 660 for the same period in 1992 (the 27-year mean is ca. 850). The cool 1992 summer may have affected staminate bud production in spruce, resulting in low pollen production in 1993.

Deposition of jack pine pollen occurred mainly in the daylight hours, when temperature and windspeed were highest and relative humidity lowest. Such diurnal periodicity also occurs in temperate (Hyde and Williams 1944; Ogden et al. 1969) and European boreal species (Käpylä 1981; Janzon et al. 1977). Rempe (1937) demonstrated that pollen trapped in the early morning mainly represents sedimentation of grains released during daylight hours.

Present and Past Pollen Deposition in Flin Flon area

Ritchie (1976) used pollen diagrams to summarize the post-glacial vegetation history of the Flin Flon, Manitoba area. Spruce species were the dominant trees between 10,500 and 8,200 years ago, with pine pollen abruptly increasing about 7000 years ago. The pollen diagram for the period 6400 years ago to present indicates 30-40% pine, 20% each for spruce, alder and birch, and < 10% for other species. These values differ somewhat from those obtained in the present study. In particular, the proportion of jack pine pollen recorded in this study is much higher than the 30-40% determined by Ritchie (1976). This difference may reflect a trend toward a drier climate in the late Quaternary, favouring jack pine due to increased forest fire frequencies. Recent logging practices may also have increased jack pine abundance. However, results obtained from gravity collectors are not directly comparable to lake sedimentation data due to interspecific differences in pollen dispersability and preservation (Sangster and Dale 1961, 1964; Prentice 1985). Pollen source area must also be considered, because sediments in large lake basins receive pollen from much larger areas than do pollen collectors in forests (Jacobson and Bradshaw 1982; Bradshaw 1981; Prentice 1985).

My results reveal some limitations inherent in reconstructing long-term vegetation dynamics of northern boreal forests from preserved pollen records. I found that aspen poplar produced small amounts of pollen relative to its abundance, whereas jack pine is overrepresented in the pollen rain. Erdtman (1943) obtained similar results in Alberta boreal forest: aspen poplar was common in the flora but poorly represented in the pollen record, whereas pines were uncommon but well represented. Thus, the absence of aspen poplar from the Flin Flon pollen record does not prove that the species was not present historically. I

conclude that paleo-vegetational reconstructions of boreal forest based on the pollen record must be interpreted with caution, because the amounts of pollen is not indicative of relative amounts of species in plant communities (cf. Davis and Goodlett 1960; Bradshaw and Webb 1985).

Chapter III
Atmospheric Deposition of Macronutrients by Pollen in the Boreal Forest

INTRODUCTION

In many temperate forest ecosystems, large quantities of tree pollen are produced over a relatively short period in early summer (Doskey and Ugoagwu 1989). Because pollen grains have high nutrient concentrations and decompose rapidly, they may be an important atmospheric source of macronutrients to terrestrial and aquatic communities (Stark 1972; Doskey and Ugoagwu 1989). Despite this, pollen has generally been overlooked in studies of forest nutrient cycling. Foster and Morrison (1976) did not consider pollen in their model of nutrient dynamics in boreal jack pine forests, despite the fact that jack pine produces considerable quantities of pollen annually. In the Jeffrey pine forests of montane Nevada, Stark (1972, 1973) found pollen to be a critical source of macronutrients to the soil litter fermentation zone during the dry, summer months. The input of macronutrients from pollen was found to have a cascading effect on nutrient dynamics by promoting litter decomposition and increasing nutrient uptake rates. Doskey and Ugoagwu (1989) determined that pine pollen was an important source of macronutrients to oligotrophic lakes in northern Wisconsin. They found that phytoplankton blooms often accompany pollen deposition events, attesting to the importance of pollen-derived nutrients to the productivity and dynamics of northern aquatic ecosystems.

In the nutrient-poor glacial outwash soils of boreal central Canada, the return of nutrients from forest to soil is critical to replenishing soil nutrient supplies

(Foster 1974). Nutrients may be transferred to the forest floor from precipitation, canopy throughfall, stemflow, litter or pollen. While forest-soil nutrient transfers have been studied in jack pine boreal forest (e.g. Foster and Gessel 1972; Foster 1974; Foster and Morrison 1976), information on the role of pollen in boreal forest nutrient dynamics is lacking. In particular, the importance of pollen in returning nutrients to the forest floor has not been determined.

In this study, I examine deposition of macronutrients by pollen in the boreal forest of west-central Manitoba. Annual deposition of tree pollen was determined along a 5.5 km transect in a mature mixed-forest stand, and in two 25-year-old regenerating jack pine stands. I estimated fluxes of pollen macronutrient based on measured rates of pollen deposition and the macronutrient content of the pollen. Further I discuss the possible importance of pollen to the cycling of macronutrients in the boreal forest.

METHODS

Study Area

The study area (Fig. 3.1) is located in west-central Manitoba, ≈ 10 km north-west of the town of Cranberry Portage (54°40' N, 101°30' W). Mean elevation is ≈ 300 m a.s.l. The climate is sub-humid continental, and the growing season extends from mid-May to early October. Mean annual precipitation is 484 mm, mean annual temperature is -0.5°C, and prevailing winds are from the north-west (climatic data from Environment Canada, based on 27-year normals (1964-1990) at Flin Flon Airport weather station, 11 km north-west of the study area).

The study area lies on the Canadian Precambrian Shield. Intense glaciation has resulted in an irregular relief characterized by granitic rocky ridges separating

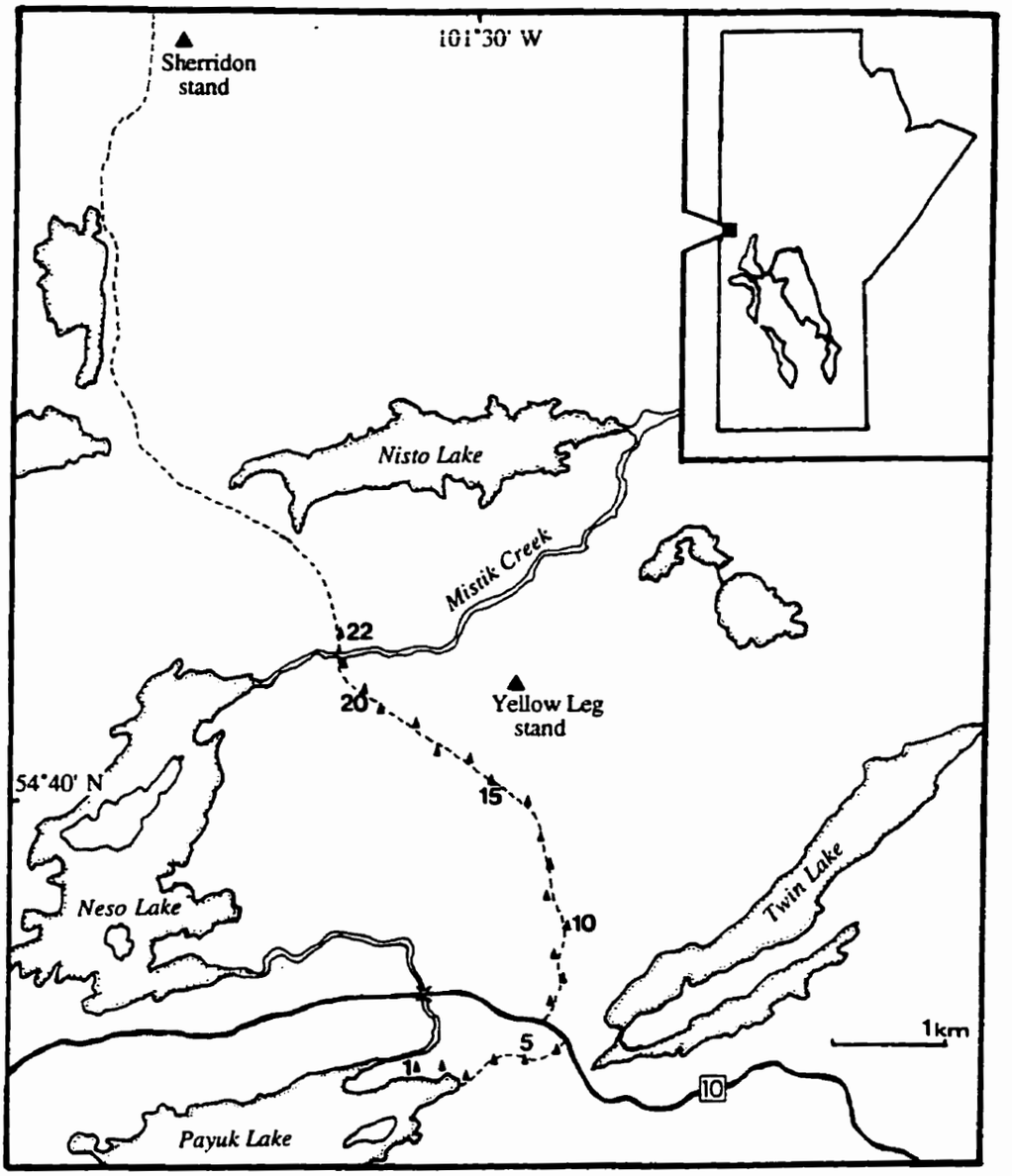

Fig. 3.1. Location of the study area in west-central Manitoba, Canada. The 5.5 km transect is located along the Sherridon Road (dotted line). The 22 sampling locations are indicated by triangles.

poorly drained depressions and narrow lakes. Exposed rock barrens are common, and soils are generally thin, of low fertility, and with a weakly developed podzolic profile. The region lies within the northern coniferous section of the boreal forest (Rowe 1972). Within the study area, black spruce (*Picea mariana* [Mill.] BSP.) is the dominant tree of poorly drained lowlands. Jack pine (*Pinus banksiana* Lamb.) stands are common on well-drained sandy sites, and on upland rock outcrops. Mixed stands of white spruce (*Picea glauca* [Moench] Voss), balsam fir (*Abies balsamea* [L.] Mill.), aspen (*Populus tremuloides* Michx.) and balsam poplar (*P. balsamifera* L.) occur under more favourable soil conditions.

Study Sites

Three study sites were sampled. The first, a 5.5 km transect through mature mixed-boreal forest, was sampled to determine annual tree pollen deposition in 'typical' mixed boreal forest. To permit ready access to pollen collectors, the transect was established along the road between Payuk Lake and Mistik Creek (Fig. 3.1). In 1992 and 1993, twenty-two sampling stations (regularly spaced, approximately 250 m apart) were established along the transect. At each sampling station, two pair of pollen collectors were established, one pair on each side of the road (88 pollen collectors in total). Each collector in a pair was located at least 10 m from the other. To minimize forest-road edge effects, pollen collectors were randomly located between 12 and 44 m from the road. In 1991, twenty-six pollen collectors at the first 13 sampling stations were sampled.

Information about the forest stand along the transect was determined using the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). At each sampling station, two transects (one on each side of the road) were located from the roadside into the forest. Ten points were located at 10 m intervals along

each transect, and at each point the distance to and basal area of the nearest tree (> 2.5 cm in diameter and > 2m in height) in each of four quadrants were measured. Summary forest stand information for the transect is presented in chapter II (Table 2.1)

Preliminary results from the 1991 sample year indicated that jack pine pollen is a major contributor to the total pollen rain in the region. To obtain more detailed information on deposition of jack pine pollen, additional collectors were established in two, 25-year-old, pure naturally-regenerating (post-fire) jack pine stands (Yellow Leg and Sherridon, Fig. 3.1). The Yellow Leg stand, located 700 m north of the transect, was sampled in 1992 (June 6 -23) and 1993 (June 1 - 18). The Sherridon stand (located 5 km north of the final transect sampling station) was sampled in 1993 (June 1 - 18). At each site, 12 pollen collectors were spaced approximately 50 m apart. Forest stand information for the Yellow Leg and Sherridon stands, based on point-centered quarter sampling (15 points located at 10 m intervals), is summarized in Table 3.1.

Pollen Deposition

Pollen deposition along the Sherridon Road transect was determined during three years. In 1991, the sampling period was May 31-June 17, and only deposition of jack pine pollen was determined. The sampling period was extended in 1992 (May 3-June 22) and pollen deposition by all tree and tall shrub species was determined. In 1993, the sampling period lasted from May 20-June 18, and deposition of jack pine and spruce pollen was determined. Voucher slides from the 1992 field season are stored at the Department of Botany, University of Manitoba.

Table 3.1. Forest composition in the two 25-year old regenerating jack pine stands (n=60 trees for each stand).

Species	Percent of individuals	Total basal area (cm^2/ha)	Relative basal area (%)
Yellow Leg stand			
Alnus crispa	3.3	232	0.8
Betula papyrifera	6.7	779	2.7
Populus tremuloides	6.7	1564	5.5
Pinus banksiana	83.3	25984	91.0
Sherridon stand			
Betula papyrifera	5.0	3152	3.5
Populus tremuioides	3.3	1326	1.5
Picea mariana	1.7	648	0.7
Pinus banksiana	90.0	85727	94.3

Durham (1946) gravity pollen collectors were employed in this study. This sampling device is approved by the National Pollen Survey Committee as the standard for sampling atmospheric pollen by the gravity method. The Durham pollen collector consists of two horizontal disks (23 cm in diameter, 15 cm apart), with the lower disk elevated 9 cm from ground level. A standard 2 x 8 cm glass slide covered with a thin film of petroleum jelly was placed on the lower disk to collect pollen. Slides were exposed for 24 hours (1991) or 48 hours (1992, 1993), and kept in a tightly sealed slide box before and following exposure to prevent contamination. Slides were examined within 24 hours under a stereo-microscope (100x magnification) to identify pollen and estimate pollen amounts. Reference slides were used to aid in pollen identification: spruce, alder, poplar and willow pollen could only be identified to genus. Pollen deposition was determining by counting all grains within a randomly selected 0.18 cm^2 area. The mean volume of fifty air-dried pollen grains was determined for each species. Absolute grain mass of each species was then determined from the mean volume estimates and the measured mass of 50 ml of air-dried pollen. Pollen counts and absolute grain mass were used to determine annual pollen deposition (g/ha) according to species.

Jack Pine Pollen Macronutrient Analysis

Total Macronutrients

In each of three years (1991-1993), three replicate samples of 1g of air-dried jack pine pollen were collected from the same location. Fresh pollen samples were obtained in the field, by gently shaking a branch (containing male cones) to which a plastic bag had been attached. Air-dried samples were digested with nitric-percloric-sulfuric acid and analyzed for nitrogen, phosphorus, potassium,

sulphur and magnesium at Norwest Laboratories, Winnipeg (Tan 1996). Total nitrogen was analyzed by the modified micro-kjeldahl method and phosphorus by the vanadomolybdo-phosphoric acid technique. Potassium, sulphur and magnesium were determined spectrophotometrically.

Water-Extractable Macronutrients

Macronutrients differ in their solubility. I determined the water-extractable portion of pollen macronutrients in order to measure operational nutrient levels produced by natural leaching. Three replicate samples of air-dried jack pine pollen were collected in the spring of 1993, in the manner described above. In the laboratory, 5 g of pollen were mixed with 500 ml of distilled water and gently stirred every hour. Water samples were taken at 0.5, 6 and 24 hours to determine total amounts of nutrients leached. The nine water samples (three replicates for each time period) were analyzed for nitrate-nitrogen, phosphate, potassium, sulphate and magnesium by Norwest Laboratories (APHA 1989). Most chemical constituents (K, S, Ca and Mg) were determined using inductively-coupled plasma (ICP) spectrometry. Nitrate-N was determined using cadmium-reduction colorimetry. Phosphate-P was analyzed by the automated colorimetry method using ascorbic acid.

RESULTS

Pollen Deposition in the Mixed Boreal Forest

In all three years (1991-93), deposition of jack pine pollen occurred during a two-week period in early to mid-June, with yearly peaks occurring on June 3, 1991, June 12-13, 1992, and June 7-8, 1993. Annual deposition of jack pine

pollen was relatively consistent among years, and was much higher in the young jack pine (Sherridon and Yellow Leg) stands than along the mixed forest transect (Table 3.2). Spruce pollen (white and black spruce) was relatively abundant along the mixed forest transect, but occurred in very low numbers in the two regenerating jack pine stands. In 1992, pollen from other species (mainly alder and poplar) contributed < 5% (by mass) of the total pollen deposition.

Macronutrient Concentration in Pollen

Nitrogen is the most abundant macronutrient in jack pine pollen, followed by potassium, phosphorus, magnesium and sulphur (Table 3.3). Macronutrient concentrations showed little variation from year to year. Total pollen nutrient deposition was relatively consistent among years (Table 3.4), with nitrogen and potassium making the greatest contribution.

Macronutrient deposition by spruce, alder, and willow pollen were also estimated for the mixed forest transect in 1992. Because pollen macronutrient concentrations were not determined for these species, data from Knight, Crooke and Shepherd (1972) for species in the same genera (*Picea abies* L. Karst., *Alnus glutinosa* (L.) Gaertn. and *A. incana* (L.) Moench, *Salix caprea* L. and *S. repens* L.) were used to obtain approximate values. Although the results must be interpreted with caution, they do suggest that black and white spruce make a substantial contribution to total deposition of pollen nutrient (Table 3.5). Values for the other species were negligible.

Pollen Deposition in Two Regenerating Jack Pine Stands

Total macronutrient deposition by jack pine pollen in the two regenerating stands is presented in Table 3.6. Because very little pollen of other species was

Table 3.2. Tree pollen deposition in the mixed-forest stand (n=88) and the two regenerating jack pine stands (n=12). Values are mean ± 1 SD, with the range given in brackets. Dashes (-) indicate that data were not collected.

Species/Year	1991 No. grains/cm^2	1991 Deposition (g / ha)	1992 No. grains/cm^2	1992 Deposition (g / ha)	1993 No. grains/cm^2	1993 Deposition (g / ha)
Mixed Forest stand						
Pinus banksiana	4476 ± 2073 (2281 - 9646)	8776	4604 ± 1316 (2595 - 7599)	9027	3980 ± 1802 (1711 - 8060)	7662
Picea mariana, *P. glauca*	-	-	1673 ± 375 (1064 - 3031)	6405	1060 ± 270 (609 - 1883)	4058
All other spp.	-	-	565 ± 510 (209 - 2986)	708	-	-
Yellow Leg stand						
P. banksiana	-	-	12533 ± 1201 (10429 - 14675)	24573	11665 ± 745 (10829 - 12987)	22852
Sherridon stand						
P. banksiana	-	-	-	-	9974 ± 550 (9172 - 11105)	19556

Table 3.3. Macronutrient concentrations in jack pine pollen collected from the study area. Values are mg per g of pollen ± 1 SD (n=3).

Year	N	P	K	S	Mg
1991	20.1±0.36	2.8±0.06	8.7±0.58	0.7±0.06	0.8±0.05
1992	19.8±0.17	2.9±0.09	8.3±0.46	0.7±0.08	0.8±0.05
1993	20.3±0.06	2.9±0.12	8.3±0.58	0.7±0.10	0.7±0.06

Table 3.4. Annual macronutrient deposition (g/ha) by jack pine pollen in the mixed forest stand.

Year	N	P	K	S	Mg
1991	176.4	24.3	76.1	6.4	7.0
1992	179.0	25.6	75.2	6.3	6.9
1993	155.8	22.5	63.8	5.4	5.6

Table 3.5. Annual macronutrient deposition (g/ha) by spruce, alder and willow pollen in the mixed forest stand.

Species*	Year	N	P	K	S	Mg
Picea mariana, P. glauca	1992	150.1	13.5	35.9	12.8	9.0
	1993	97.0	8.5	22.7	8.1	5.7
Alnus spp.	1992	7.28	0.35	0.45	0.37	0.15
Salix spp.	1992	0.17	0.016	0.012	0.01	0.008

* Pollen nutrient data from Knight et al. 1972: *Picea abies, Alnus glutinosa /A. incana,* and*Salix caprea /S. repens.*

Table 3.6. Macronutrient deposition (g/ha) by jack pine pollen in the two 25-year-old regenerating jack pine stands.

Site	Year	N	P	K	S	Mg
Yellow Leg	1992	487.4	70.5	204.8	17.2	18.8
	1993	464.6	67.0	190.4	16.0	16.8
Sherridon	1993	397.6	57.4	163.0	13.7	14.3

collected, the values presented represent stand totals. Total macronutrient deposition is higher in the regenerating jack pine stands than in the mixed forest. Values for the Yellow Leg stand were similar in 1992 and 1993, and the 1993 value was higher than that obtained at the Sherridon stand.

Water-Extractable Pollen Macronutrients

The majority of water-extractable pollen macronutrients were solubilized within the first half-hour (Table 3.7). After 24 hours, the water-extractable portion was highest for potassium (88.4% of total extractable), magnesium (68.6%), sulphur (67.3%) and phosphorus (62.1%). By contrast, only 0.1% of NO_3-nitrogen was leached from jack pine pollen after 24 hours.

DISCUSSION

Macronutrient Deposition by Pollen Rain

Jack pine was disproportionately represented in the pollen rain. Along the mixed-forest transect, the relative basal area of jack pine was 17.6% but the species contributed 56% to the annual pollen biomass. Annual deposition of jack pine pollen ranged from 7.7-9.0 kg/ha along the mixed forest transect, and from 19.6-24.6 kg/ha in the two regenerating jack pine stands. These values are greater than the 0.9-3.0 kg/ha range reported for Jeffrey pine stands in Nevada (Stark 1973), but fall within the broad 3.5-80.0 kg/ha range estimated for white and red pine (*P. strobus* L., *P. resinosa* Ait.) stands in northern Wisconsin (Doskey and Ugoagwu 1989).

Table 3.7. Water-extractable macronutrient concentrations in jack pine pollen over time. Values are mg per g of pollen ± 1 SD (n=3).

I.T.*	Macronutrient concentration				
	N	P	K	S	Mg
0.5	0.02 ± 0.001	1.48 ± 0.05	7.27 ± 0.03	0.408 ± .007	0.49 ± .004
6	0.02 ± 0.001	1.60 ± 0.08	7.23 ± 0.15	0.414 ± .003	0.50 ± .011
24	0.02 ± 0.002	1.82 ± 0.25	7.37 ± 0.04	0.471 ± .014	0.50 ± 0.10

* Immersion time (hours).

Nutritional Perspective of Pine Pollen

Macronutrient concentrations of pine pollen are 2-3 times higher than those of fresh conifer needles, and 2-5 times higher than litterfall (Stark 1973). Total macronutrient levels in jack pine pollen were generally similar to pollen of other pine species. Total nitrogen and phosphorus concentrations were similar to the closely-related *P. contorta* Doug. (Stark 1972), and to *P. resinosa* and *P. strobus* (Doskey and Ugoagwu 1989), but potassium concentrations were somewhat higher and sulphur lower. Values for total nitrogen, potassium and phosphorus were higher than those reported for *P. contorta*, *P. mugo* Turra. and *P. sylvestris* L. by Knight, Crooke and Shepherd (1972), but values for sulphur were lower. While these results may reflect between-species variation, it is also possible that differences in soil-nutrient availability, or in the nutrient extraction method used, could account for the differences.

Distribution and Cycling of Nutrients in Jack Pine Stands

Jack pine has lower nutrient requirements than other northern conifers, enabling the species to maintain acceptable growth rates on low-fertility sites (Morrison 1973). Nonetheless, by age 30 jack pine stands in northern Ontario become phosphorus and nitrogen limited because of low rates of litter decomposition (Foster and Morrison 1976). In northern Ontario stands, annual per ha nutrient uptake rates were estimated at 26 kgN, 1.7 kgP, and 15.2 kgK. My corresponding values for nutrient deposition by pollen (Table 3.7, 1992 Yellow Leg stand) are 0.49 kgN, 0.07 kgP, and 0.20 kgK, suggesting that pollen contributes relatively little to overall stand nutrient dynamics. Pollen deposition, however, occurs over a brief, two-week period in early to mid-June. In addition, pollen grains are broken down within two months (Stark 1972), suggesting that

pollen may be an important source of macronutrients during the critical early summer growth period. By comparison, the mean turnover rate of litter in the pine forests of boreal North America is ≈ 10 years (Prescott, Corbin and Parkinson 1989).

Stark (1972, 1973) concluded that pine pollen enhances decomposition by providing an early-summer macronutrient pulse to decomposers in the litter fermentation zone. I believe that a similar pollen-mediated 'nutrient cascade' may be operating in boreal forest ecosystems. The pollen rain may be important in ombrotrophic bogs, lakes and other habitats where the principal external source of nutrients is atmospheric deposition. In northern Wisconsin, a significant proportion of the annual atmospheric deposition of phosphorus (20%) and potassium (45%) is attributable to pollen (Doskey and Ugoagwu 1989).

Because phosphorus is limiting in terrestrial boreal ecosystems (Foster and Morrison 1976), pollen decomposition may provide 'pulse' source of phosphorus in early summer. The water-soluble fraction of phosphorus deposited by jack pine pollen in the Yellow Leg stand represents > 70% of total throughfall phosphorus, and > 6% of litterfall phosphorus, reported for jack pine stands in northern Ontario (Foster and Morrison 1976). In a study of jack pine canopy throughfall, Foster (1974) noted "leaching of large quantities of phosphorus from pollen ... during May and June", but treated this as a "contaminant" and excluded it from further analysis. It is also possible that the high early summer phosphorus throughfall levels reported by Foster and Gessel (1972) are attributable to pollen contamination.

Macronutrient Fluxes by Pollen Rain to Lake Ecosystem

Pollen macronutrient deposition may also be important to aquatic systems. In early June (1991-1993), brilliant yellow layers of jack pine pollen occurred along the margins of Payuk Lake (Fig. 3.1) and other water bodies in the study area. Because pre-Cambrian boreal lakes are oligotrophic (Rawson 1960), pollen deposition may be an important 'pulse' nutrient source for aquatic plants, including phytoplankton. Doskey and Ugoagwu (1989) report that phytoplankton blooms in northern Wisconsin lakes often coincide with periods of pine pollen dispersal. This indicates that episodic nutrient input from pollen contributes to the ecological dynamics of northern lakes.

Macronutrient deposition by pollen is concentrated both temporally and spatially. Pollen deposition is highly episodic, and nutrient concentrations and decomposition rates of pollen grains are high (Stark 1973). In contrast, decomposition rates of jack pine litter are much lower, resulting in the accumulation of considerable amounts of litter over time (Foster and Morrison 1976; Prescott, Corbin and Parkinson 1989). Although the annual contribution of nutrient mass by pollen is small compared to that of litterfall (Stark 1972; Foster and Morrison 1976), the rapid turnover rate of pollen nutrients combined with episodic deposition suggest that pollen may play a disproportionate role in boreal forest nutrient cycling. Future studies should be directed toward obtaining a better understanding of the effect of tree pollen nutrient pulses on the functioning of terrestrial and aquatic boreal ecosystems.

Chapter IV
Chytrid Distribution in Selected Boreal Manitoba Sites

INTRODUCTION

Although chytrids are ubiquitous and have been collected across Arctic to tropical latitudes, relatively little direct information exists regarding chytrid activity in boreal forest and bog habitats. Sphagnum bogs are considered to be rigorous environments because of high acidity and limited naturally occurring substrates (Lund 1934; Lange 1978). Despite such limitation, bogs are one of the richest sources of bizarre types of chytrids (Sparrow 1966). Furthermore, bogs are also high in chytrid diversity (Miller 1965a).

Subsequent to publication of Sparrow (1952), a few papers dealing with chytrids from these habitats have been published. For example, chytrids were reported from forest and bog sites in the transition zone between mixed deciduous and boreal forest of northern Michigan (Johns 1956; Sparrow and Koch 1959; Sparrow et al. 1965; Gaertner and Sparrow 1966; Dogma 1969, 1970). Johnson and Howard reported zoosporic fungi from freshwater and bog habitats in Iceland and Norway (Howard 1968; Howard and Johnson 1969; Johnson 1973, 1975, 1977). Booth (1969, 1971a, 1971b) studied zoosporic fungi in forest and bog soils of coastal British Columbia and Booth and Barrett (1971, 1976) reported chytrids from acidic soils of the Canadian high-arctic. In general, systematic study of chytrids from boreal forest soils and microhabitats, other than bogs, seems to be rare.

Based on their nutritional capabilities, these fungi are important biodegraders of cellulose, chitin, and keratin, which are resistant to decay by many microorganisms (Powell 1993). Pollen exine, readily available in boreal forest and bog habitats, is a particularly refractory substrate that chytrids are able to digest to gain access to the nutrient-rich contents (Sparrow 1960). The major chemical components of the pollen wall is sporopollenin, which is composed of carotenoids and carotenoid esters. In a comprehensive investigation of pollen and spores degraded by chytrids, gymnosperm pollen (especially pine) walls were shown to be highly susceptible to local digestion (Goldstein 1960).

Studies on the role of fungi in pollen degradation in forest soils are limited. Pollen may be considered an important source of nutrients for tree growth and its degradation (hence, nutrient mobilization) in dry sites has been reported to be more effectively carried out by filamentous fungi than by chytrids (Stark 1972). (In fact, Stark suggested that chytrids were generally unimportant in pollen degradation in contrast to filamentous fungi). As the activity of chytrids has not been systematically studied in the range of boreal forest micro-environments or in forest ecosystems in general, it is not known if Stark's conclusion about pollen degradation by chytrids and filamentous fungi in dry sites is generally true. Furthermore, the role of pollen degradation in forest nutrition has yet to be elucidated.

In a series of two chapters, including this one, I will report on a spatial and temporal study of chytrids from soils collected in non-randomly and randomly selected boreal forest microhabitats with the overall aim to provide information on the possible importance and role of chytrids in forest nutrition over a range of naturally occurring environmental conditions. Specifically the aim of this study is: i) to record the levels of chytrid infestation of pollen placed as bait with soils

collected from selected diverse boreal Manitoba sites; ii) to observe distributional patterns of pollen infesting chytrids across boreal forest sites; and iii) to describe the species composition of pollen inhabiting chytrids that occur in soils within different types of litter.

MATERIALS AND METHODS

Study Area

The Mistik Creek study area (Fig. 4.1) is located in west-central Manitoba, Canada (54°39' to 54°50' N; 101°27' to 101°32' W). The climate is sub-humid continental and prevailing winds are from the northwest. The growing season, based on a 4°C index, lasts from early May to early October. Mean annual precipitation is 484 mm and mean annual temperature is -0.5°C. Average land elevation is about 300 m above sea level.

The region lies on the Canadian Precambrian Shield. As a result of intensive glaciation, relief is irregular with rocky parallel ridges separating poorly drained depressions and narrow lakes. Drift depositions on the uplands are thin in some places and absent in others where rock barrens of Precambrian granites and gnesisses are exposed. Soil fertility is low with a weakly developed podzol profile.

The study area includes the northern coniferous section of the boreal forest (Rowe 1972). Within the area, black spruce (*Picea mariana* [Mill.] BSP) is the dominant tree in poorly drained lowlands. Jack pine (*Pinus banksiana* Lamb.)

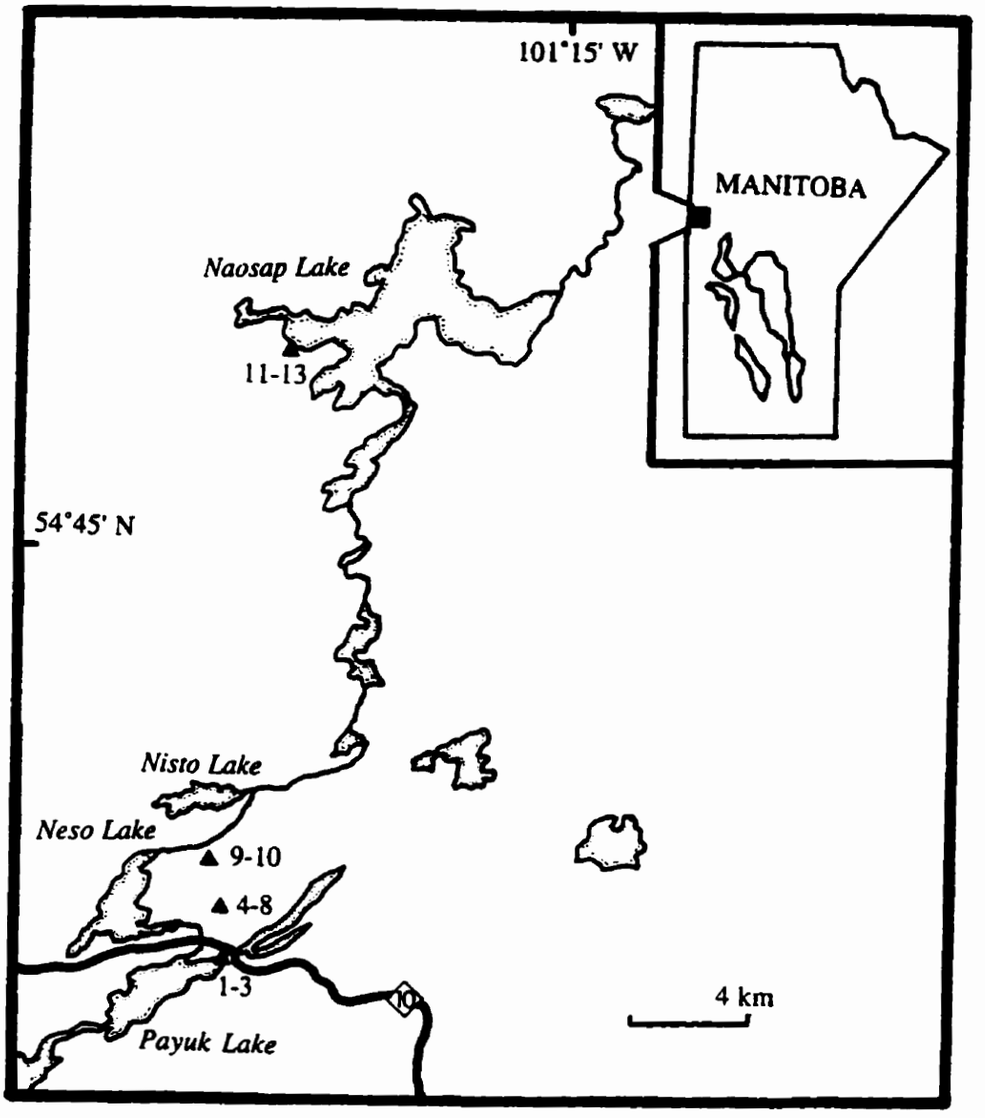

Fig. 4.1. Location of the study area (Mistik Creek) in west-central Manitoba, Canada. Sites are designated by numbers: **1** = Balsam Fir ; **2** = Mature Pine ; **3** = Poplar ; **4** = Pine Ridge ; **5** = Spruce ; **6** = Bog ; **7** = Swale ; **8** = Alder ; **9** = Young Pine ; **10** = Bare Sand ; **11** = Naosap Forest ; **12** = Naosap Riser; **13** = Naosap Beach. Closely approximated sites are mapped as groups indicated by triangles.

stands are common on well-drained, sandy sites and on upland, rock outcrops. Mixed stands of white spruce (*Picea glauca* [Moench] Voss), balsam fir (*Abies balsamea* [L.] Mill.), aspen (*Populus tremuloides* Michx) and balsam poplar (*P. balsamifera* L.) occur under more favourable soil conditions.

Soil collection, Pollen baiting and Laboratory observation

Soil samples were collected on August 21, 1993. The collections were made from the top 3 cm of litter and soil over 13 sites (Fig. 4.1). Detailed designations and descriptions of the thirteen selected sites are presented in Table 4.1. In each site 5 replicate soil samples were collected. Within 48 hours after soil collection, one gram of soil from each replicate was placed in an individual petri dish and covered to a depth of 1 cm with deionized water. Air dried jack pine pollen (*Pinus banksiana*), collected from the same region as the soil samples, was added to the water as bait. Baited samples were maintained at room temperature (ca. 21°C).

After baiting, the pollen was surveyed for chytrids every other day for a ten day period and individual species were noted (Repeated observation of developing and discharging chytrid thalli were required for identification of species). During the survey period, levels of pollen infestation (% of 100 grains surveyed) were determined and recorded for each observation date. Infestation by each taxon on the fifth observation date (at ten days) was used to represent the infestation levels by all individual species. Pollen infestation levels from the various soils were also determined at the fifth observation date (after 10 days of incubation) and calculated as percentage of grains infested by all species. Species diversity was identified as the number of chytrid species occurring in each site. Species dominance for various soils was determined as the taxon with

the highest pollen infestation levels relative to all other infesting species in each specific site.

Similarity of Chytrid Assemblages between Sites

The V coefficient of association (Kreb 1972) was calculated for between-site comparisons of fungal assemblages, where:

$$V = \frac{ad - bc}{\sqrt{(a+b)(c+d)(a+c)(b+d)}}$$

(a = the number of taxa common to sites 1 and 2, b = the number of taxa exclusive to site 1, c = the number of taxa exclusive to site 2, and d = the number of taxa excluded from both sites 1 and 2). A site with one chytrid species, Naosap beach sands, was excluded in this analysis.

RESULTS

Litter Types

Four litter groups were recognized based on litter and soil types in the study area (Table 4.1). These included: i) mixed (leaf and needle pieces) litter with high needle content; ii) mixed litter with high broad leaf content; iii) loamy soil with broad leaf content and, iv) needles on exposed sand. Mixed litter with high needle content characterized the Pine Ridge, Naosap Forest, and Naosap Riser sites. Mixed litter with broad litter content was encountered in the Mature Pine, Poplar, Spruce, Bog, and Alder sites. Swale was in loamy soil with broad leaf litter. Needles on exposed sand were found in Young Pine, Bare Sand, and Balsam Fir sites.

Table 4.1. Site numbers, site designations, and descriptions of the selected 13 sites.

No.	Designations	Descriptions
1	Balsam Fir	Mixed litter (high needle content) on sand from a balsam fir and white spruce stand.
2	Mature Pine	Mixed litter soil from a mature 65-yr. old jack pine stand mixed with patches of alder and black spruce.
3	Poplar	Mixed litter (high broad leaf content) soil from a trembling aspen and alder stand.
4	Pine Ridge	Lichens and mixed litter (high needle content) soil from a jack pine ridge.
5	Spruce	Mixed litter with some mosses and soil from a black spruce stand.
6	Bog	Mosses and wet mixed litter soil from a black spruce and alder stand.
7	Swale	Exposed soil from a willow and *Carex* swale.
8	Alder	Mixed litter from an alder stand.
9	Young Pine	Needle litter on sand from under trees in a young (25-yr.) regenerating jack pine stand.
10	Bare Sand	Sand from open areas (not under young trees and with sparse needle litter) in a young (25-yr.) regenerating jack pine stand.
11	Naosap Forest	Mixed litter (high needle content) soil from a jack pine stand along the margin (5m from the beach) of Naosap lake (mixed with alder).
12	Naosap Riser	Mixed litter (high needle content on loam) from a riser edge located above (2m) and away (2.5m) from Naosap lake beach strand. Collections from a jack pine (mixed with alder) forest edge fronting lake beach.
13	Naosap Beach	Unvegetated regosolic material (sands) from open washed beach

Pollen Infestation by Site

Total infestations of pollen by chytrids ranged from 5.8% to 90.2% from the various soils (Table 4.2). Three groups were designated based on pollen infestations (i.e. those with high, medium, and low pollen infestation levels). The high pollen infestation group (> 40%) includes five sites: Young Pine, Naosap Forest, Bog, Naosap Riser, and Pine Ridge sites. The medium infestation group (20 to 40%) is comprised of Mature Pine, Balsam Fir, Alder, and Spruce sites. The low infestation group (< 20%) encompasses: Poplar, Naosap Beach, Swale, and Bare Sand sites.

The highest pollen infestation occurred in soils collected from the Young Pine site, with 90.2% of pollen bait infested by chytrids (Table 4.2). The second highest pollen infestation, 79.4%, was observed on pollen bait added to Naosap Forest soils. Both of these sites have high needle content in the litter. Infestations by endobiotic chytrids (i.e. *Olpidium* spp.) were low in soil collections from all sites (0% to 9.6%). The highest endobiotic chytrid infestations were found in samples taken from the Poplar site.

Chytrid Diversity and Distribution

Species diversity tended to be higher in soils with higher pollen infestation and lower in soils with lower pollen infestation (Table 4.2). Soils with high infestation (> 40%) had 4 to 6 species from each collection site (mean ≈ 5 spp.). Soils with medium and low infestation (< 40%) had 1 to 5 species (mean ≈ 3 spp.). The greatest diversity (6 spp.) was observed in soils from sites with high needle litter content (Naosap Forest, Naosap Riser and Pine Ridge sites). Lower diversities were generally observed in mineral soils or soils with a limited organic horizon comprised, at least in part, of broad leaf litter.

Table 4.2. Pollen infestation (% grains infested after 10 days of incubation) of jack pine pollen added as bait to flooded soil samples collected in selected boreal Manitoba sites. Pollen infestation values are mean ± S.E. (n=5).

Sites	Total grains infested (%)	Number of chytrid species
Young Pine	90.2 ± 2.5	4
Naosap Forest	79.4 ± 11.5	6
Bog	56.0 ± 10.6	5
Naosap Riser	52.0 ± 13.0	6
Pine Ridge	46.2 ± 17.7	6
Mature Pine	37.2 ± 19.0	3
Balsam Fir	34.4 ± 8.6	2
Alder	34.2 ± 12.6	5
Spruce	30.8 ± 14.8	4
Poplar	12.4 ± 6.3	2
Naosap Beach	11.4 ± 5.1	1
Swale	10.4 ± 4.5	4
Bare Sand	5.8 ± 2.3	2

Specimens of *Olpidium* spp., the most wide spread of the chytrids in this study, were observed in pollen bait placed with soil from 11 of the 13 sites. *Rhizophydium pollinis-pini* (Braun) Zopf and *Phlyctochytrium reinboldtae* Persiel were found from only four sites making them the most restricted in distribution (Table 4.3). *Rhizophydium pollinis-pini* was found in Spruce, Alder, Bog, and Poplar sites which were typified by mixed litter with broad leaf content. *Phlyctochytrium reinboldtae* occurred in litter and soils from Swale, Naosap Forest, Naosap Riser, and Pine Ridge sites, all of which are high in needle litter content.

Chytrid Dominance

Four species showed maximum infestations of pollen over the 13 sites (Table 4.3). *Rhizophydium sphaerotheca* Zopf (*sensu* Booth 1971b) dominated (relative frequency) in collections from Naosap Beach (100%), Bare Sand (96.6%), Mature Pine (94.1%), Balsam Fir (82%), Pine Ridge (60.2%), Swale (55.8%), and Naosap Risers (51.9%). *Chytriomyces annulatus* Dogma dominated in Young Pine (75%) samples. *Chytriomyces poculatus* Willoughby and Townley dominanced in peat or soils from Bog (72.1%) collections, Naosap Forest (57.9%), and Alder (42.7%) stands. *Olpidium* spp. dominated in soils of Poplar (77.4%) groves. High dominance (76 to 100%) was seen in low chytrid infestation sites with low diversity, while lower dominance (≤75%) was observed in high infestation sites with high diversity.

Coefficients of Association

Based on coefficient of association values (Fig. 4.2), three site groups are distinguishable. Young Pine, Bare Sand, and Balsam Fir represent the first associated group, which is characterized by exposed sand or needle litter on

Table 4.3. Pollen infestations (%) by chytrid species placed with soils collected from the selected sites in boreal Manitoba. (Maximum infestation for each site is indicated in bold face). (Naosap Lake beach sands yielded only one species, *Rhizophydium sphaerotheca*, at 11.4 % infestation).

	Young Pine	Bare Sand	Balsam Fir	Swale
Olpidium spp.	1.2	0.2	0	3.0
Chytriomyces annulatus	**68.0**	0	6.2	0
Phlyctochytrium papillatum	12.6	0	0	0
Rhizophydium sphaerotheca	8.4	**5.6**	**28.2**	**5.8**
Chytriomyces poculatus	0	0	0	1.4
Rhizophydium pollinis-pini	0	0	0	0
Phlyctochytrium reinboldtae	0	0	0	0.2
Total pollen infestation (%)	90.2	5.8	34.4	10.4

	Naosap Forest	Naosap Riser	Pine Ridge	Spruce
Olpidium spp.	1.4	5.6	1.2	0.6
Chytriomyces annulatus	20.6	4.0	14.0	0
Phlyctochytrium papillatum	0.8	2.8	0.8	2.8
Rhizophydium sphaerotheca	10.2	**27.0**	**27.8**	0
Chytriomyces poculatus	**46.0**	12.0	2.2	**26.4**
Rhizophydium pollinis-pini	0	0	0	1.0
Phlyctochytrium reinboldtae	0.4	0.6	0.2	0
Total pollen infestation (%)	79.4	52.0	46.2	30.8

	Mature Pine	Alder	Bog	Poplar
Olpidium spp.	0.2	1.6	2.2	**9.6**
Chytriomyces annulatus	0	7.8	0.2	0
Phlyctochytrium papillatum	2.0	0.8	0.2	0
Rhizophydium sphaerotheca	0	0	0	0
Chytriomyces poculatus	**35.0**	**14.6**	**40.4**	0
Rhizophydium pollinis-pini	0	9.4	13.0	2.8
Phlyctochytrium reinboldtae	0	0	0	0
Total pollen infestation (%)	37.2	34.2	56.0	12.4

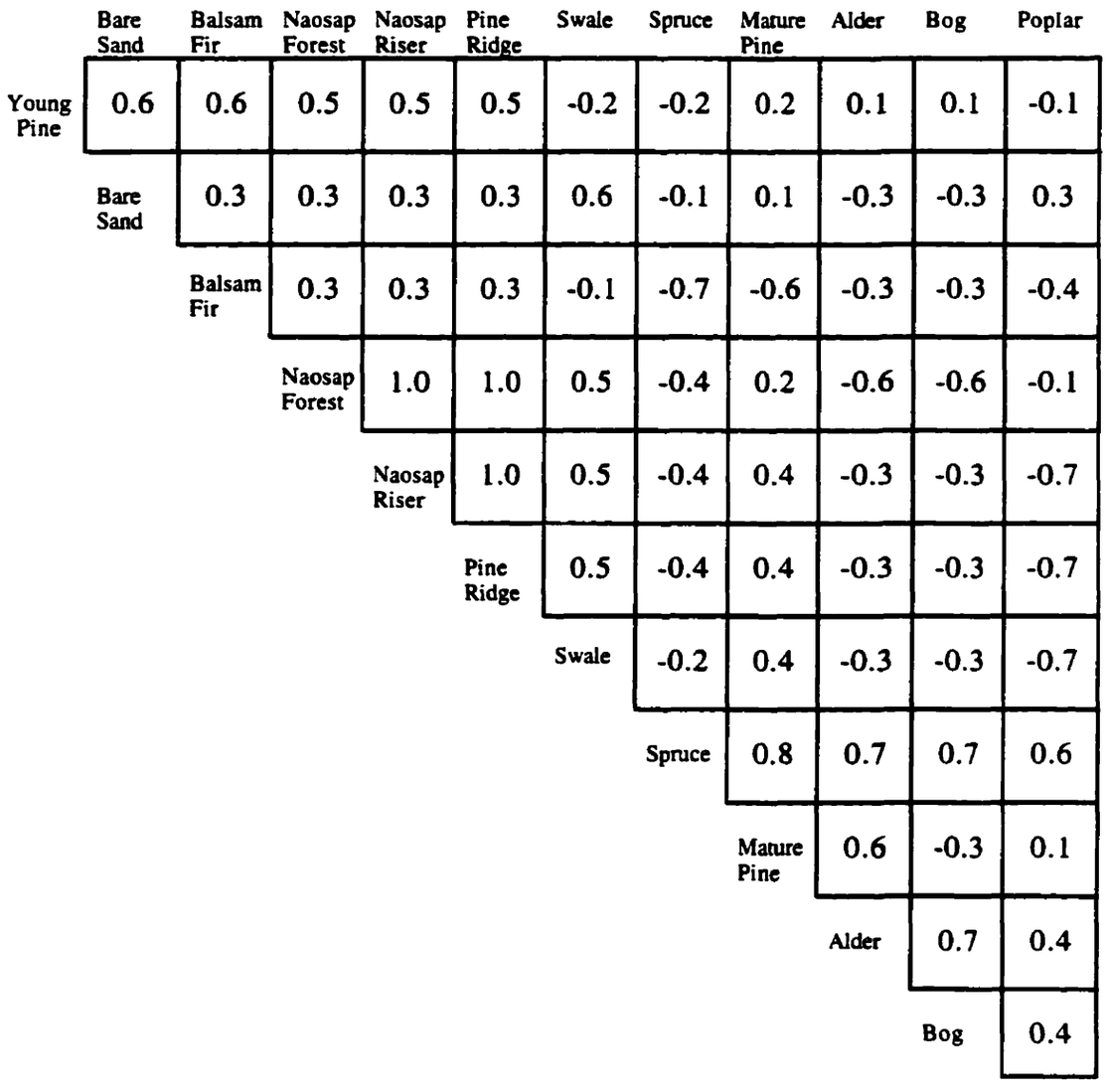

Fig. 4.2. Coefficients of association for fungal assemblages in site parings (A coefficient value ≥ 0.6 is considered to indicate strong association).

sand. (The reader may wish to consult Table 4.1 for site description data). The second associated group includes Naosap Forest, Naosap Riser, and Pine Ridge sites, which are strongly tied by high needle litter content. Spruce, Mature Pine, Alder, and Bog sites represent the third associated group, which has mixed litter with alder litter content.

Species in Common

Based on comparisons of chytrid assemblages in baited soils from selected sites in west-central boreal Manitoba, two major site groups can be recognized (Fig. 4.3). The first of these includes the Young Pine, Bare Sand, Balsam Fir, Naosap Forest, Naosap Riser, Pine Ridge, and Swale sites. *Rhizophydium sphaerotheca* is common to these sites. This group may be divided into two subgroups. The first subgroup includes Young Pine, Bare Sand, and Balsam Fir sites having, *R. sphaerotheca* in common, and the second subgroup includes Naosap Forest, Naosap Riser, Pine Ridge, and Swale sites with *R. sphaerotheca*, *Chyriomyces poculatus* and *Phlyctochytrium reinboldtae* in common. Spruce, Mature Pine, Alder, Bog, and Poplar sites represent the second major group. This group is characterized by the presence of *Olpidium* spp. and *C. poculatus* along with the absence of *R. sphaerotheca*.

DISCUSSION

Pollen Infestation by Site

In boreal sites, occurrence of increased organic matter in soils is reflected in pH values below neutrality. Soils rich in organic matter usually have an ameliorated moisture regime, whereas soils with an increased mineral content have pH values

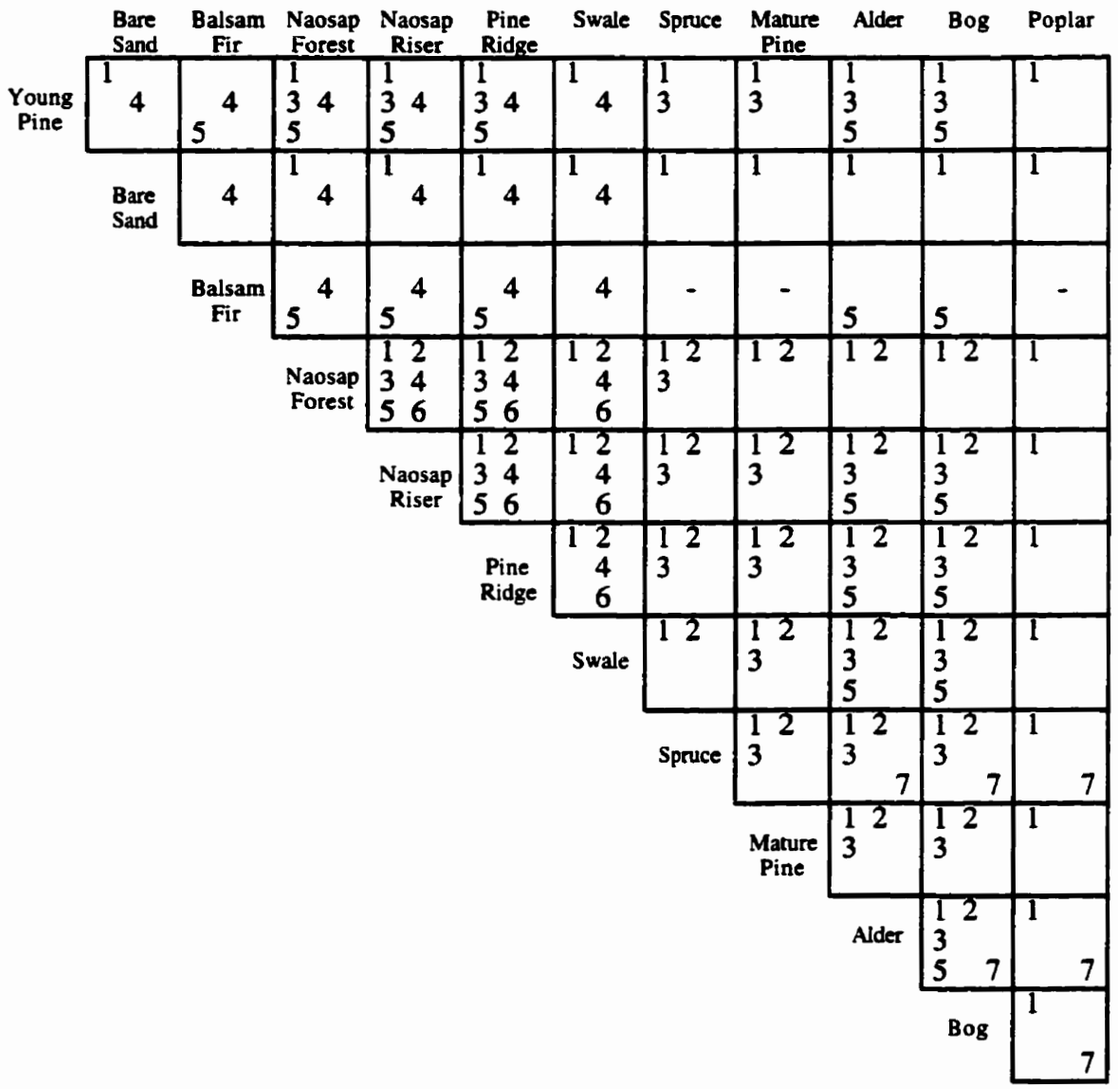

Fig. 4.3. Chytrid species in common among site parings (n = 66) of selected boreal Manitoba sites. Species are numbered: **1** = *Olpidium* spp., **2** = *Chytriomyces poculatus*; **3** = *Phlyctochytrium papillatum*; **4** = *Rhizophydium sphaerotheca*; **5** = *Chytriomyces annulatus*; **6** = *Phlyctochytrium reinboldtae*; **7** = *Rhizophydium pollinis-pini*.

above neutrality and rapidly changing soil moisture regimes. As in previous studies (Remy 1948; Willoughby 1964, 1965; Booth 1971c; Booth and Barrett 1976), my results showed higher levels of pollen infestation in soils rich in organic matter and lower infestation levels from mineral soils. Each site with high infestation levels was characterized by litter with high needle content while medium infestations were in sites with mixed (needle and broad leaf) litter. Mineral soil or soil with limited organic matter yielded low levels of pollen infestation. In addition, the presence, or absence, of litter and the type of litter correlated with levels of pollen infestation. These observations may reflect pH, moisture regimes or interactions of the chytrids with other abiotic and biotic elements.

Species Diversity

During the summer ice wedge polygons are the most acidic, warmest and driest soils in the studied ecosystem (Booth and Barrett 1976). My results substantiated the findings of the high-Arctic study with high diversities (6 spp.) in soils from warm and dry sites. The high needle content of my warm and dry sites suggests that they were also acidic. Observation of high diversity (5 spp.) in my bog samples coincides with previous reports (Miller 1965a; Sparrow 1966) of a substantial variety of chytrids in this ecosystem. Lower diversity of chytrids from mineral soils also has been previously observed (Gaertner 1954). Species diversity in soils from Mistik Creek study region seems to be, in part, determined by types of litter or the presence or absence of litter.

Chytrid Distribution and Dominance

As observed in an earlier study (Booth 1971c), *Rhizophydium sphaerotheca* Zopf was collected from mesic to xeric, middle to low pH, warm soils. This species

also was fairly widely distributed across soil and litter types (Booth 1971c, 1979; Booth and Barrett 1971, 1976).

The occurrence of *Chytriomyces poculatus*, from low pH soils in the Mistik Creek area confirmed to the distributional pattern reported in the type description (Willoughby and Townley 1961) and subsequently (Willoughby 1965; Dogma 1969; Booth and Barrett 1971). *Chytriomyces annulatus*, which came from low pH litters on sands in my study area, was originally described (Dogma 1969) from acidic soils and later found from leaf litter on regosolic sands (Booth and Barrett 1976; Booth 1979).

Originally isolated (Sparrow 1952) from riverbank soils in a Michigan coniferous forest, *Phlyctochytrium papillatum* Sparrow is generally absent from mixed litter sites in the Mistik Creek region. *Rhizophydium pollini-pini* has been reported from mixed litter habitats (Booth and Barrett 1971, 1976) as is the case in my study. Narrow in ecological range (Booth 1979), *Phlyctochytrium reinboldtae* Persiel occurs in the dry sites of the my study area that are high needle litter.

In Mistik Creek sites with high needle content or needles on sand, *Rhizophydium sphaerotheca* is generally the dominant species. The tendency for this chytrid to be dominant in acidic sites is seen in the work of Booth and Barrett (1971, 1976). Originally reported from broad leaf litter (Willoughby and Townley 1961), *Chytriomyces poculatus* is dominant in mixed litter with high content of angiospermous leaf pieces in my study area. Litter from these sites is less acidic than the high needle content litter.

Species Assemblages and Litter Types

Based on coefficients of association and species in common among species across the collection sites, it is possible to relate dominant species to species assemblages in site groups. *Rhizophydium sphaerotheca* typifies site group I (Young Pine, Bare Sand, and Balsam Fir). *Chytriomyces poculatus*, *Phlyctochytrium reinboldtae* and *Rhizophydium sphaerotheca* are common to site group II (Naosap Forest, Naosap Riser, Pine Ridge, and Swale). Finally *Chytriomyces poculatus* and *Olpidium* spp. occur together in site group III (Alder, Bog, Mature Pine, Popular, and Spruce).

These species assemblages in the site groups suggest that the chytrids are distributed according to litter and soil types (cf. group I, needles on sands or sandy soils; group II, mixed litter high in needle content on loamy soils and group II mixed litter with high angiospermous leaf content on loamy soils. Roberts (1963) pointed out that the type of decaying vegetation might represent a more decisive factor determining the distribution of zoosporic fungi than simple hydrogen ion content. Although hydrogen ion content has been demonstrated to be correlated with chytrid distribution (Willoughby 1965; Booth 1971c; Booth and Barrett 1976), it is possible that the substratum characteristics, e.g. broad leaf litter, mixed leaf litter or needle leaf litter, and availability of litter, may be as critical as pH in describing their distribution in boreal forest sites. Furthermore, it is possible that litter types and characteristics are more meaningful than simple pH in accounting for spatial distribution of chytrids in nature. A previous study on the ecology of lower saprophytic fungi indicated that distinct aquatic and terrestrial floras could be distinguished in the order Chytridiales (Willoughby 1961). My study gave some indication that edaphic factors might control the yields and explain the apparently discontinuous distribution of certain very

common species. I conclude, therefore, that the typical boreal forest chytrid species found in my study are characteristic of the micro-flora where soil pH is low and associated with the ground litter types.

Chapter V

Factors Affecting Pollen Infestation by Chytrids in Boreal Manitoba

INTRODUCTION

Tree and tall shrub pollen deposition occurs from late April to mid June in the boreal forest of west-central Manitoba, Canada. Maximum pollen deposition in the region is 25 kg/ha/season in regenerating stands of *Pinus banksiana* Lamb. (jack pine) and in mixed stands pollen rain delivers 16.1 kg/ha/season (Chapters II and III, this dissertation). Although the annual contribution of nutrient mass by pollen is small compared to total litterfall (Stark 1972; Foster and Morrison 1976), the sudden nutrient enrichment of the forest floor by throughfall and stemflow (Foster and Gessel 1972; Foster 1974) suggests that pollen plays an important role in boreal forest nutrient cycling.

Pollen contributes water soluble (i.e. phosphorus at mean levels of 99.4 and potassium at 23.7 g/ha/season) nutrients to the forest by leaching within 24 hours of aqueous contact (Chapter III, this dissertation). These macronutrients from pollen stimulate litter decomposition (Stark 1972, 1973). In addition to contribution of macronutrients, pollen is a significant source of organic nitrogen. Stark (1973) states that after spring pollen rain, grains require two months to settle from the litter surface into the fermentation zone where there is an increase in nitrogen and phosphorus. This suggests that nitrogen and phosphorus are available and mobilized by chytrids as well as other decomposing fungi as pollen moves downward by gravity and waterflow. It is known that chytrids play an

important part in the decay of pollen under various conditions (Gaertner 1954; Goldstein 1960; Roberts 1963; Miller 1965a; Sparrow 1966; Skvarla and Anderegg 1972; Booth 1973c; Lange 1978).

The general ecology of soil chytrids has been previously studied by a number of workers, notably Remy (1948), Reinboldt (1951), Gaertner (1954, 1968), Apinis (1964) and Willoughby (1965). Many of these studies are primarily synecological, but some are autecological and deal with factors affecting distribution of specific chytrids (Remy 1948; Gaertner 1954; Willoughby 1961, 1965; Booth 1971c; Booth and Barrett 1976; Kenkel and Booth 1992).

Reports of Remy (1948) and Gaertner (1954) indicate that the distribution of soil inhabiting species is not related to pH. Reinboldt (1951) concludes that soil moisture rather than soil temperature is the more potent factor in determining the numbers of individuals present in German soils. Conversely, Willoughby (1961) compares three lake margins and concludes that high moisture, concentration of organic matter, exchangeable cation concentration, and pH affect the number of taxa in sites. Willoughby further indicates that substrate-fungus relations should be carefully considered in ecological work.

Subsequent studies have correlated several chytrid species with various environmental variables including pH and substrate types (Booth 1971c; Booth and Barrett 1976). Booth (1971c) relates environmental factors (i.e. pH, organic matter, bulk density, osmolarity, Ca^{2+}, Mg^{2+}, and Na^{+}) to the occurrence and frequency of specific chytrid species. Booth and Barrett (1976), in their study of zoosporic fungi from acidic soils of a High Arctic ecosystem, concludes that factors such as soil moisture, temperature, and organic matter content, as well as pH, determine species diversity in High Arctic ecosystems. They also report that

species diversity is greatest in mesic and warm soils and species composition of water-logged soils differ from that of dry soils.

Little ecological information, however, is available regarding factors that affect distribution of chytrids in boreal forest soils. The goal of this study is to provide information on the abiotic and biotic factors affecting chytrid distribution in soils from the boreal forest in west-central Manitoba.

MATERIALS AND METHODS

Study Area

Soil samples were collected along the 5.5-km transect on either side of the Payuk Lake road continuing to the Sherridon road between Provincial highway 10 and Mistik Creek (Fig. 5.1). The transect ran through mixed boreal forest representative of Precambrian west-central Canada. (Environmental description of the collection region is provided in Chapters II, III and IV of this dissertation.)

Twenty-two soil sampling stations, regularly spaced 250 m apart, were established along the Sherridon road for the 1992 and 1993 collections. At each sampling station, two pairs of randomly located soil collection sites, at least 10 m apart, were established on each side of the road. Collections were made on seven sampling dates (26 June, 22 July, and 3 November 1992; 21 May, 17 June, 21 August, and 9 October 1993). Soil collections for pollen infestation were made from the top 3 cm of litter from 88 sites along the 5.5-km transect. Litter and soil types were characterized for each collection site on the initial collecting date (26 June 1992).

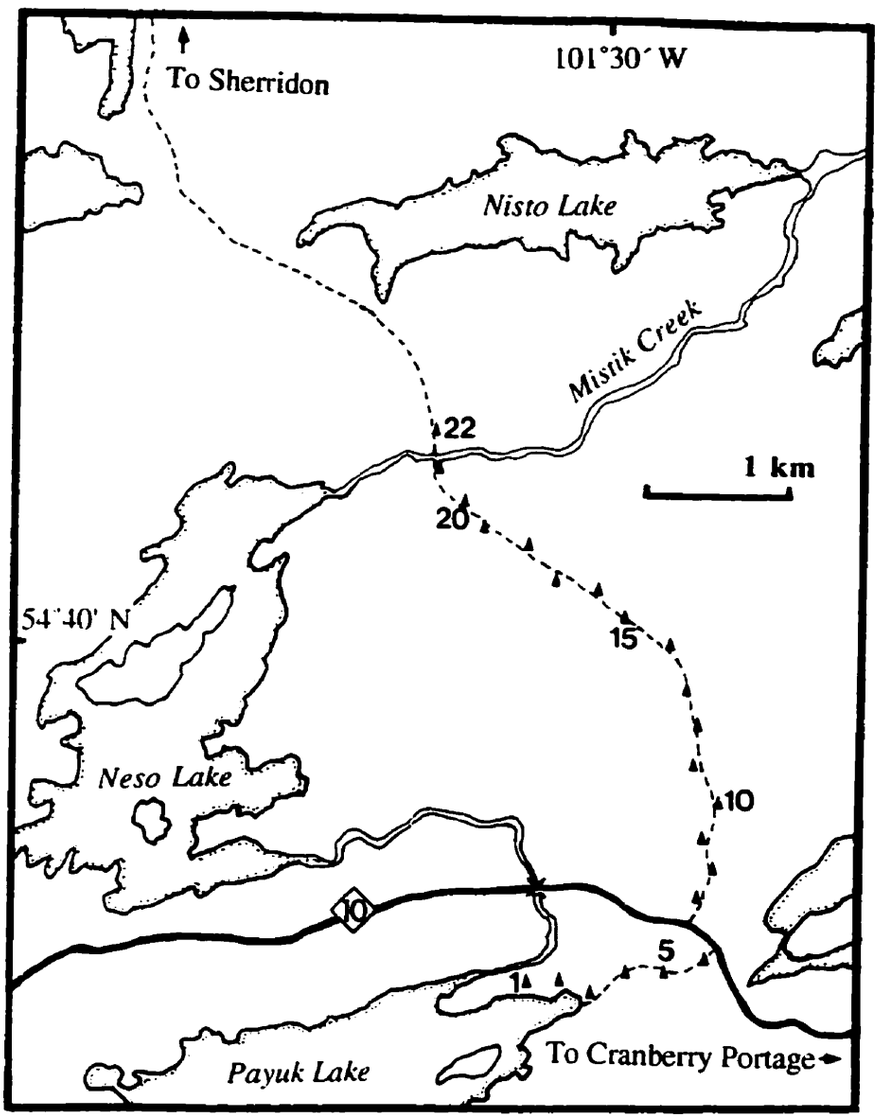

Fig. 5.1. Location of the study area (Mistik Creek) in west-central Manitoba, Canada. Sites are designated by number.

Study Area Climate

Climate of the study area (54°40' N, 101°30' W) is continental and prevailing winds are from the northwest. According to Köppen (1967), this region is Dcf (subarctic) and is characterized by severe winters with less than four months warmer than 10°C (daily mean temperatures). The growing season, based on a 4°C index, lasts from early May to early October. Mean annual precipitation is 484 mm and mean growing season temperature is 13.4°C. Environment Canada data (from the Flin Flon Airport, 11 km north-west of the study area) indicates monthly mean temperature of -5°C to 17°C and total precipitation ranges of 11 mm to 140 mm during the period of April-November 1992 and April-October 1993 (Fig. 5.2).

Woody Vegetation, Dominance and Openness

Woody vegetation at the 22 sampling stations along the transect was determined using the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). (The reader may wish to consult Chapter II of this thesis for more detail on the vegetation sampling methods employed in this study.) An importance index was calculated by taking the mean of the additive of relative density, dominance and frequency values. From the index, woody vegetation dominance was assigned based on importance: i) dominant species over 40% in importance; ii) subdominant species with 39-20% importance, and iii) common species at 19-15% importance.

Values for site openness were determined by counting direct sunlit, decimeter intervals on tapes placed on the forest floor, crossed at 2.5 m and oriented exactly on north to south and east to west magnetic compass headings. Light interception was measured between 1100 and 1300 hours on 23-26 June 1992 to

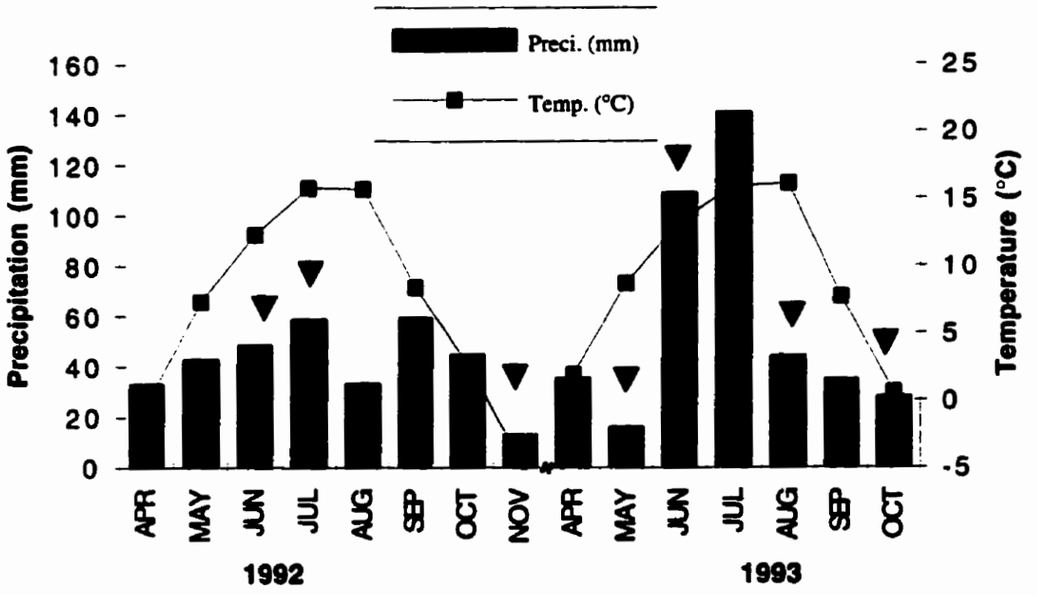

Fig. 5.2. Monthly mean temperature (black squares) and total precipitation (shaded bars) at Flin flon Airport, Manitoba, for the period: April - November, 1992 and April - October, 1993. (data obtained from Environmental Canada). Arrows indicate months of soil sampling for chytrids.

approximate incoming sunlight in the period of the summer solstice zenith. The total number of sunlit decimeter intervals, of the 100 sampled (50 along each tape), was taken to account for the percent openness of the canopy at the site. (Sunlit spots were also assumed to represent site forest floor area exposed to direct pollen fall.)

Soil Analysis

Two soil cores (98 cm^3 each) were extracted, on 9 October 1993, from each of the collecting sites to a depth of 5 cm, placed in plastic bags and immediately analyzed for moisture content. Soil moisture was calculated as the percentage loss of water mass from field soil dried at 105°C for 24 hours. Dried soil was then returned to University of Manitoba laboratories for further processing. Soil pH was measured in a 5:1 (5 parts distilled water to 1 part soil) suspension using a glass electrode pH meter. Soil organic content was gravimetrically determined by carbon loss after combustion at 430°C for 18 hours.

Pollen Deposition

Seasonal (3 May through 22 June, 1992) pollen deposition by 10 woody species (i.e. *Pinus banksiana* Lamb. *Picea mariana* (Mill.) BSP., *Picea glauca* (Moench) Voss, *Alnus crispa* (Ait.) Pursh, *Alnus rugosa* (Du Roi) Spreng, *Populus tremuloides* Michx., *Populus balsamifera* L., *Betula papyrifera* Marsh., *Larix laricina* (Du Roi) K. Koch, and *Salix* spp.) was determined for each of the 88 sites using Durham (1946) gravity pollen collectors. Specific collecting methods and means of analysis utilized in determination of total seasonal pollen are presented in Chapter II of this dissertation. (Pollen deposition data are presented in Appendix III, this dissertation)

Chytrid Sampling and Data Processing

Detailed pollen baiting and laboratory study techniques are previously presented in Chapter IV. Chytrids on pollen baits added to soils were observed every 48 hours during a 10 day study period. Pollen infestations by epibiotic chytrids for each collecting date were determined by calculating the mean percentage (± S.E.) of finds (number of infested grains) divided by the starts (100 pollen grains observed at each of the 88 sites). Infestation data for each of the 88 sites over 7 collecting dates and individual chytrid taxa is found in Appendix V. Pollen infestation values in mixed leaf litter, sphagnum peat and needle litter for each of the collecting dates were derived from: i) separating sites according to litter types (i.e. mixed leaf, 36 sites; peat, 22 sites; and needle, 30 sites); ii) determining the total number of infested (by combined chytrid taxa) grains for each of the litter types and collecting dates; and iii) dividing the number of infested grains by the total number of grains observed for each litter type (i.e. mixed leaf, 3600; peat, 2200; and needle, 3000) and collecting date.

Similar aggregate data was prepared for *Chytriomyces annulatus* Dogma, *Chytriomyces poculatus* Willoughby and Townley, *Rhizophydium sphaerotheca* Zopf (sensu Booth), and *Phlyctochytrium papillatum* Sparrow by processing separate litter types and the sites for each specific taxon on the collection dates. For example, pollen infestation in needle litter for a selected species on one of the collection dates is calculated as the number of finds of the taxon for that date divided by the starts (3000 in the case of needle litter sites).

RESULTS

Site Characteristics

Descriptions of tree dominance, openness, litter and/or substratum types and pH are presented in Table 5.1. (Additional site details, inc. general description, site slope gradient and direction, woody species present, tree density and frequency, basal area/tree species, trees/ha, basal area/ha, canopy height, canopy cover, forest floor cover, soil type, soil organic matter, and soil moisture, are presented in Appendices I, II and IV of this dissertation.)

Dominant woody vegetation in the Payuk Lake/Mistik Creek study area is clearly represented by *Picea mariana* (dominant in 20 of 44 transects). *Picea mariana* is also sub-dominant in a further 15 transects and common in three others. *Pinus banksiana* is dominant in three transects, sub-dominant in 10 transects and common in three others. *Picea glauca*, dominant in two transects, is sub-dominant in four and common in two others. *Populus tremuloides* is sub-dominant in 10 and common in four other transects. The remaining woody species, *Abies balsamea*, *Alnus crispa*, *Alnus rugosa*, *Betula papyrifera*, *Larix laricina*, *Populus balsamifera* L. and *Salix* spp., are sub-dominant in three or fewer sites.

Litter types, resulting from site vegetation, are mixed (whole coniferous needles and needle fragments mixed with angiospermous leaf pieces), deciduous leaf predominant (angiospermous leaf pieces) and needle predominant (whole coniferous needles and needle fragments). Moisture tends to be higher in peat

Table 5.1. Site designations and soil collection descriptions.

Site #	Collection description	Soil pH	Openess[1]	Vegetation dominance[2]
1R1	mixed litter on loam	6.1	14	**P. glauca, +P. tremuloides, +A. balsamea*
1R2	mixed litter on loam	6.3	36	
1L1	mixed litter on loam	5.6	30	*+P. tremuloides, +P. glauca, A. crispa*
1L2	mixed litter on loam	5.6	46	
2R1	mixed litter on loam	5.3	33	*+P. glauca, P. tremuloides, A. balsamea*
2R2	mixed litter on loam	6.0	24	
2L1	mixed litter on loam	5.6	30	*+P. glauca, +P. tremuloides*
2L2	mixed litter on loam	5.9	58	
3R1	loam	5.6	95	*+P. glauca, +P. mariana, P. tremuloides*
3R2	loam	5.1	84	
3L1	mixed litter on loam	5.8	16	**P. glauca, +P. mariana*
3L2	needle litter on loam	4.3	46	
4R1	needle litter on loam	4.0	66	**P. mariana, A. crispa, P. tremuloides*
4R2	needle litter on loam	4.4	69	
4L1	needle litter on loam	4.5	18	**P. mariana, +P. tremuloides, P. glauca*
4L2	needle litter on loam	4.1	34	
5R1	needle litter on loam	4.0	26	**P. banksiana, +P. mariana*
5R2	needle litter on loam	4.1	41	
5L1	needle litter on loam	4.6	59	**P. banksiana, A. crispa*
5L2	needle litter on loam	4.5	47	
6R1	mixed litter on loam	5.0	28	**P. mariana, +P. tremuloides, A. crispa*
6R2	mixed litter on loam	6.1	24	
6L1	needle litter on loam	4.7	34	*+P. tremuloides, +P. banksiana, P. mariana, A. crispa*
6L2	mixed litter on loam	5.8	37	
7R1	mixed litter on loam	5.4	40	*+P. tremuloides, +P. mariana*
7R2	needle litter on rock	4.8	48	
7L1	mixed litter on loam	6.0	14	**P. mariana, +P. tremuloides*
7L2	broad leaf litter on loam	6.7	72	
8R1	mixed litter on loam	5.6	35	*+P. mariana, +P. banksiana*
8R2	mixed litter on loam	5.9	53	
8L1	mixed litter on rock	4.8	42	**P. banksiana, +P. mariana*
8L2	needle litter on rock	4.3	90	
9R1	broad leaf litter on loam	5.7	28	*+P. balsamifera, B. papyrifera, P. tremuloides*
9R2	broad leaf litter on loam	5.6	46	
9L1	wet Sphagnum/peat	5.4	48	**P. mariana*
9L2	wet Sphagnum/peat	4.6	23	
10R1	needle litter on rock	4.4	74	**P. mariana, +P. banksiana*
10R2	mixed litter on rock	4.8	67	
10L1	mixed litter on rock	5.2	44	**P. mariana, Salix sp.*
10L2	needle litter on rock	4.5	38	
11R1	loam	6.3	60	*+P. banksiana, +P. mariana*
11R2	needle litter on rock	5.0	81	
11L1	dry Sphagnum/peat	5.0	20	**P. mariana*
11L2	dry Sphagnum/peat	4.8	31	
12R1	mixed litter on loam	5.8	16	**P. mariana, P. glauca*
12R2	mixed litter on loam	5.2	52	
12L1	needle litter on loam	5.3	34	*+P. glauca, A. rugosa, P. mariana*
12L2	loam	5.3	92	
13R1	wet Sphagnum/peat	4.8	73	*+P. mariana, +L. laricina, A. crispa*
13R2	wet Sphagnum/peat	4.3	34	
13L1	dry Sphagnum/peat	4.2	49	**P. mariana*
13L2	dry Sphagnum/peat	4.5	19	

14R1	needle litter on rock	5.1	100	*+P. mariana, +P. banksiana, A. crispa*
14R2	loam	5.1	81	
14L1	mixed litter on rock	5.0	87	**P. mariana, +P. banksiana*
14L2	needle litter on rock	4.3	48	
15R1	mixed litter on loam	4.7	40	*+A. crispa, +B. papyrifera, P. banksiana, P. mariana*
15R2	needle litter on loam	3.7	84	
15L1	dry Sphagnum/peat	6.2	29	**P. mariana, B. papyrifera*
15L2	dry Sphagnum/peat	6.5	50	
16R1	dry Sphagnum/peat	4.4	49	**P. mariana*
16R2	dry Sphagnum/peat	3.9	45	
16L1	mixed litter on loam	5.7	52	*+P. mariana, L. laricina, B. papyrifera, A. crispa*
16L2	mixed litter on loam	5.8	38	
17R1	dry Sphagnum/peat	3.7	55	**P. mariana*
17R2	dry Sphagnum/peat	3.7	66	
17L1	dry Sphagnum/peat	5.7	69	**P. mariana, A. crispa*
17L2	dry Sphagnum/peat	3.8	69	
18R1	needle litter on rock	4.1	55	*+P. banksiana, +P. mariana, +A. crispa*
18R2	needle litter on rock	4.5	36	
18L1	dry Sphagnum/peat	4.7	61	*+P. mariana*
18L2	dry Sphagnum/peat	4.9	96	
19R1	needle litter on rock	4.6	47	*+P. mariana, +A. rugosa, P. banksiana*
19R2	needle litter on rock	4.5	60	
19L1	wet Sphagnum/peat	5.0	80	**P. mariana, +L. laricina*
19L2	wet Sphagnum/peat	5.3	39	
20R1	needle litter on rock	4.9	54	*+P. mariana, +P. tremuloides, P. banksiana*
20R2	needle litter on rock	4.4	52	
20L1	wet Sphagnum/peat	5.6	69	**P. mariana, +A. rugosa, Salix sp.*
20L2	wet Sphagnum/peat	5.9	83	
21R1	needle litter on rock	3.9	72	**P. mariana, +P. banksiana*
21R2	needle litter on rock	4.3	83	
21L1	mixed litter on loam	6.1	82	*+P. balsamifera, +A. crispa, +P. tremuloides, +Salix sp.*
21L2	loam	6.3	85	
22R1	needle litter on rock	4.1	20	**P. mariana, +P. banksiana*
22R2	needle litter on rock	4.4	39	
22L1	mixed litter on rock	4.8	24	**P. mariana, +P. banksiana*
22L2	needle litter on rock	4.4	14	

[1]Openess expressed as % area open to incoming zenith sunlight

[2]Vegetation dominance

*dominant = > 40 % importance; +subdominant = 39 - 20 % importance: common = 19 - 15 % importance

and litter on soil (loam) sites than in litter on regosolic material (granitic rock) sites (Fig. 5.3).

Over the sampling sites, openness ranges from 100% (all of the sampled area exposed to incoming solar radiation) to 14% (86% closed tc incoming radiation) (Table 5.1). Mean collecting site openness is 50.4%. Total pollen deposition of major contributing woody species does not correlate linearly (r= .17) with the openness of sites. Mean 1992 total pollen deposition for all 88 sites combined is 6842 (± 1579) grains/cm^2 (= 16.1 kg/ha) and deposition across the individual sites ranges from 4288 grains/cm^2 (10.2 kg/ha at site 13R2) to 11521 grains/cm^2 (23.4 kg/ha at site 21L2). Weak trends of decreased basal area, soil organic matter, moisture, and pH with increased openness are evidenced in the data (Table 5.2). Soil (litter) moisture and organic matter are strongly correlated (r= .84), a trend partially demonstrated by arrangement or soil moisture ranges and means derived from grouped litter types as previously described. Soil and peat pH values over the 88 collecting sites range from strongly acidic (3.7) to nearly neutral (6.7) (Table 5.1). Mean pH for all sites is ~5.0. Basal area and pH are weakly positively correlated (Table 5.2).

Contrasting sites, the more open locations (>40%) tend to have lower values of basal area, organic matter, moisture and pH. The relatively more closed sites (<40%) tend to be higher in basal area, organic matter, moisture and pH. Needle litter and peat characterize the open sites while mixed and broad leaf litter tend to be most frequent on soils of closed sites.

Spatial Considerations: Pollen Infestations and Environmental Factors

Infestations of pollen ranged from a low of 2.0% (site 8R1) to a high of 77.9% (site 22R2) (Table 5.3). Standard error values reflected considerable within site

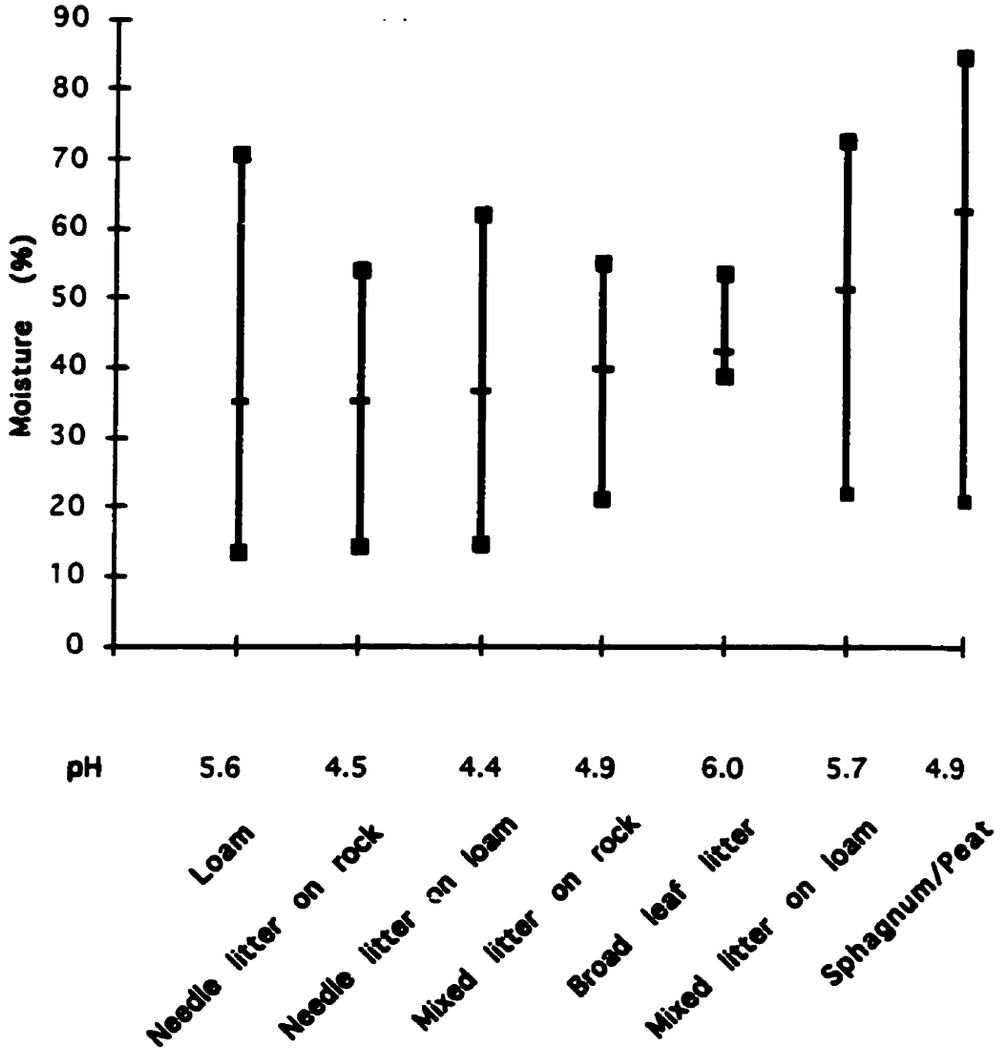

Fig. 5.3. Relationship between litter-soil types and soil moisture levels in boreal Manitoba microhabitats (Ranges and means are indicated by hatched lines).

Table 5.2. Pearson product-moment correlation coefficients of environmental factors and pollen infestation.

Factors	Pollen infestation (%)	Soil moisture (%)	Soil organic matter (%)	Openess (%)	Tree basal area (m^2/ha)
Soil moisture	-0.13				
Soil organic matter	-0.19	**0.84**			
Openess	**0.34**	-0.22	-0.22		
Tree basal area	**-0.44**	0.07	0.25	-0.26	
Soil pH	**-0.71**	0.02	-0.01	-0.29	**0.37**

Table 5.3. Epibiotic chytrid infestation (% of grains infested after 10 days of incubation) of jack pine pollen added as bait to flooded soil samples collected along a gradient of microhabitats in boreal Manitoba over seven 1992 / 93 dates. Infestation values are mean ± S.E. (n=7).

Sites	Grains infested (%)	Sites	Grains infested (%)	Sites	Grains infested (%)	Sites	Grains infested (%)
1R1	3.0 ± 2.2	6L1	21.9 ± 12.9	12R1	24.4 ± 13.3	17L1	57.0 ± 15.1
1R2	7.4 ± 4.9	6L2	18.0 ± 12.9	12R2	22.7 ± 11.4	17L2	48.1 ± 9.9
1L1	9.3 ± 3.8	7R1	3.7 ± 2.7	12L1	49.3 ± 11.4	18R1	58.4 ± 10.2
1L2	9.1 ± 5.6	7R2	33.7 ± 11.0	12L2	10.7 ± 9.6	18R2	73.3 ± 8.5
2R1	14.6 ± 7.4	7L1	12.0 ± 6.5	13R1	64.9 ± 10.7	18L1	35.6 ± 13.8
2R2	4.6 ± 2.1	7L2	3.0 ± 1.4	13R2	56.7 ± 5.5	18L2	42.0 ± 12.9
2L1	2.9 ± 1.5	8R1	2.0 ± 1.2	13L1	68.1 ± 8.5	19R1	43.4 ± 7.7
2L2	9.9 ± 7.1	8R2	16.0 ± 5.3	13L2	36.4 ± 15.3	19R2	49.0 ± 14.1
3R1	21.9 ± 5.9	8L1	25.4 ± 5.4	14R1	50.7 ± 11.8	19L1	57.6 ± 10.5
3R2	18.9 ± 9.8	8L2	57.9 ± 9.0	14R2	15.1 ± 12.0	19L2	47.3 ± 10.9
3L1	10.1 ± 9.5	9R1	14.7 ± 11.2	14L1	17.0 ± 7.3	20R1	36.9 ± 9.4
3L2	45.9 ± 11.5	9R2	0.3 ± 0.2	14L2	63.6 ± 8.2	20R2	62.9 ± 10.3
4R1	40.9 ± 12.4	9L1	15.4 ± 9.5	15R1	18.9 ± 9.3	20L1	29.1 ± 8.2
4R2	32.6 ± 13.3	9L2	28.6 ± 16.3	15R2	37.4 ± 12.9	20L2	16.7 ± 4.7
4L1	20.0 ± 12.0	10R1	51.3 ± 11.6	15L1	28.0 ± 9.8	21R1	55.4 ± 14.2
4L2	29.3 ± 12.8	10R2	7.6 ± 3.5	15L2	43.3 ± 7.1	21R2	47.3 ± 12.5
5R1	51.0 ± 12.2	10L1	13.6 ± 6.2	16R1	55.9 ± 10.5	21L1	16.4 ± 8.1
5R2	15.4 ± 5.8	10L2	19.7 ± 5.8	16R2	44.1 ± 10.6	21L2	3.4 ± 1.3
5L1	23.7 ± 8.4	11R1	14.3 ± 6.2	16L1	22.3 ± 8.9	22R1	68.4 ± 12.4
5L2	45.6 ± 9.0	11R2	44.6 ± 12.3	16L2	9.3 ± 9.1	22R2	77.9 ± 5.6
6R1	11.0 ± 6.8	11L1	17.6 ± 11.0	17R1	52.9 ± 9.8	22L1	16.7 ± 10.9
6R2	12.9 ± 9.0	11L2	23.1 ± 11.3	17R2	36.9 ± 13.5	22L2	49.7 ± 12.8

variation for mean percentages of infestation. Generally, chytrid infestations increased from the Payuk Lake road sites (sites 1 - 7) to the sites near Mistik Creek crossing of Sherridon road (sites 16 - 22). (Detailed chytrid infestation data for the sites over the seven sampling dates are available in Appendix V of this dissertation.)

Among the pollen infesting chytrids encountered in the study area are: *Chytriomyces annulatus* Dogma, *Chytriomyces poculatus* Willoughby & Townley, *Olpidium* spp., *Phlyctochytrium* sp.-*Phlyctochytrium aurilae* Ajello, *Phlyctochytrium planicorne* Atkinson, *P. papillatum* Sparrow, and *P. reinboldtae* Persiel, *Rhizophydium pollinis-pini* (Braun) Zopf, *R. sphaerotheca* Zopf (sensu Booth 1971b). *Septosperma rhizophidii* Whiffen., parasitic on *C. annulatus R. pollinis-pini* and *R. sphaerotheca*, appeared infrequently in soils from acidic (pH <5.0) sites. (The reader may wish to refer to Appendix VI of this dissertation for morphological and ecological description of these species.)

Groupings of soil-litter types showed maximum infestations of pollen by chytrids in needle litter on rock sites and minimum infestations in angiospermous (broad) leaf litter (on loam) sites (Fig. 5.4). Generally, infestations were higher in needle litter and sphagnum/peat sites than in mixed litter, exposed loam or angiospermous leaf litter sites.

A trend in decreasing pollen infestation with increasing pH can be seen across the site groups aligned by means and ranges. Evidence of a moderately strong negative correlation of pollen infestation by chytrids and soil pH is further demonstrated in Table 5.2 (r= -.71). Openness and tree basal area are weakly correlated with chytrid pollen infestation.

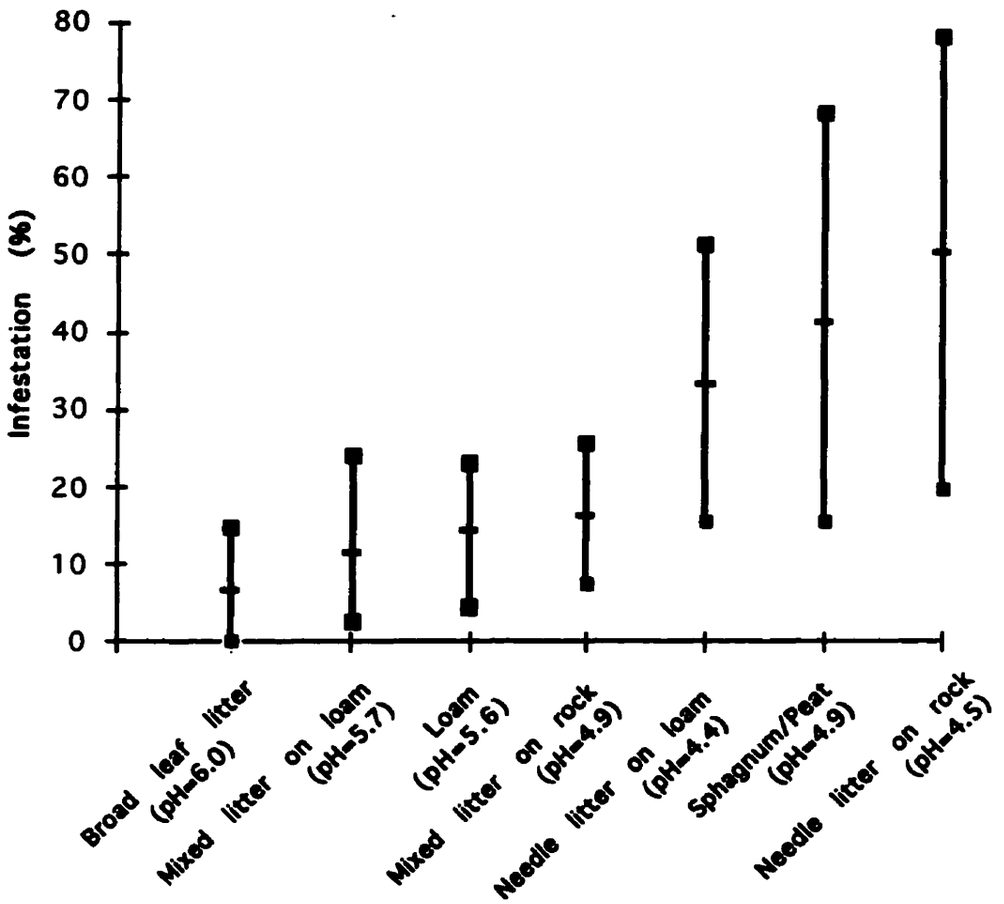

Fig. 5.4. Relationship between types of litter-soil and pollen infestation (% of grains infested after 10 days of incubation) of jack pine pollen added as bait to flooded soil samples collected in boreal Manitoba microhabitats (Ranges and means are indicated by hatched lines).

Infestations of pollen by individual chytrid species across the range of soil pH demonstrated a similar trend (Fig. 5.5). *Chytriomyces poculatus* and *Rhizophydium sphaerotheca* were spread across the pH range of the study sites. *Phlyctochytrium papillatum* and *Chytriomyces annulatus* tended to infest pollen at higher percentages than other chytrids and were associated with lower pH sites. Conversely, *Phlyctochytrium reinboldtae* infested pollen baits added to soils from higher pH sites and tended, along with *R. sphaerotheca* , to yield some of the lowest infestation levels.

Temporal Considerations: Litter Types and Pollen Infestation

Pollen infestations by combined chytrids were generally higher in soils from the more acidic needle litter and peat sites than from the mixed leaf litter sites (Fig. 5.6). Chytrid seasonality was clearly indicated by pollen infestation levels from mixed leaf litter sites. Infestations in soils from these sites were higher in November 1992 and May 1993 litter collections than from samples taken in the summer months. Seasonal highs were not as clearly demonstrated by infestation levels from needle litter and mixed leaf litter sites, even though the highest level of infestations across all seven dates and the three litter types were observed from November 1992 needle litter collections.

Temporal Consideration: Pollen Infestation by Selected Species in Litter Types

Species selected, *Chytriomyces annulatus*, *C. poculatus*, *Phlyctochytrium papillatum*, and *Rhizophydium sphaerotheca*, are those showing combined (from 61,600 starts) spatial (over 88 sites) and temporal (on seven collecting dates) pollen infestations greater than 5%. All other epibiotic chytrids encountered in this study demonstrated temporally and spatially combined infestation levels of less than 2%. (The reader may wish to consult Appendix V for raw data on pollen

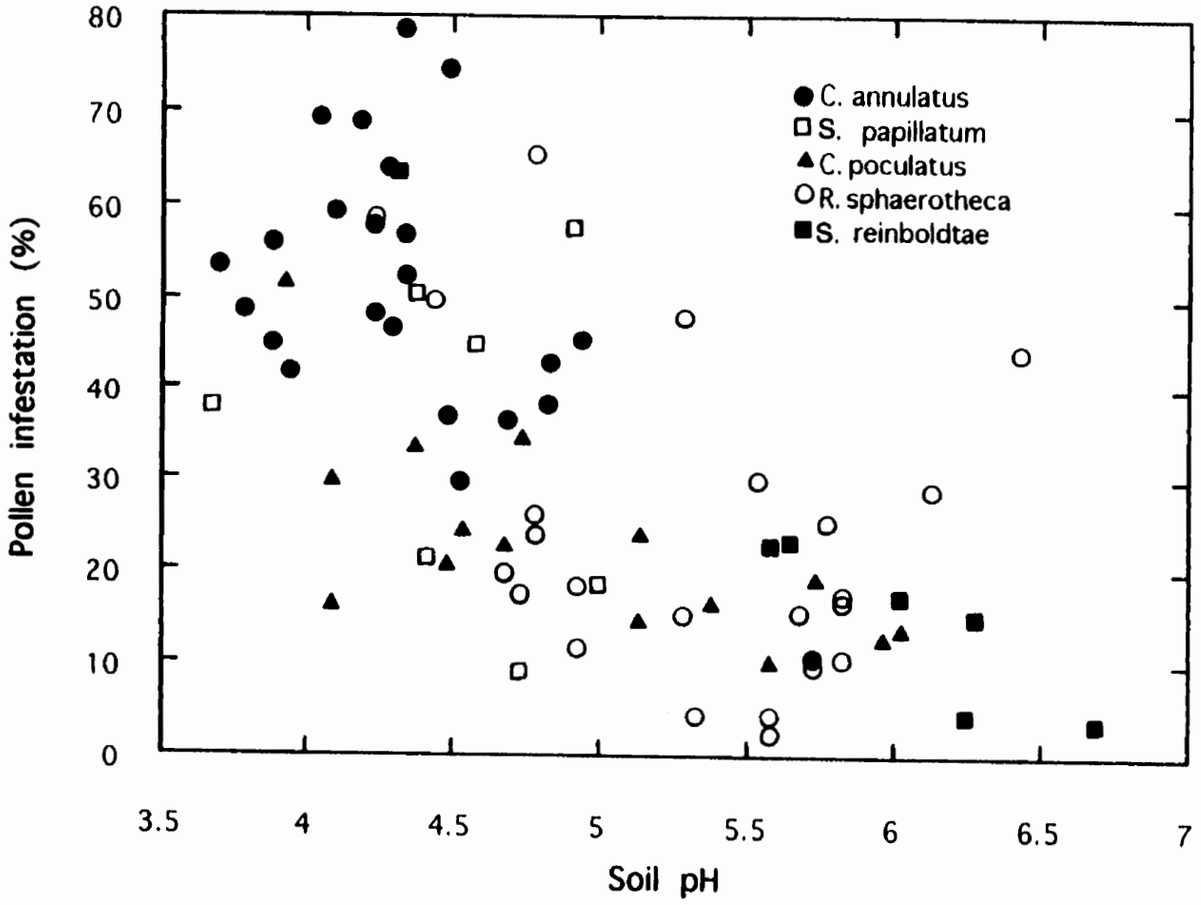

Fig. 5.5. Plots of pollen infestation and individual chytrid occurrences correlated with soil pH.

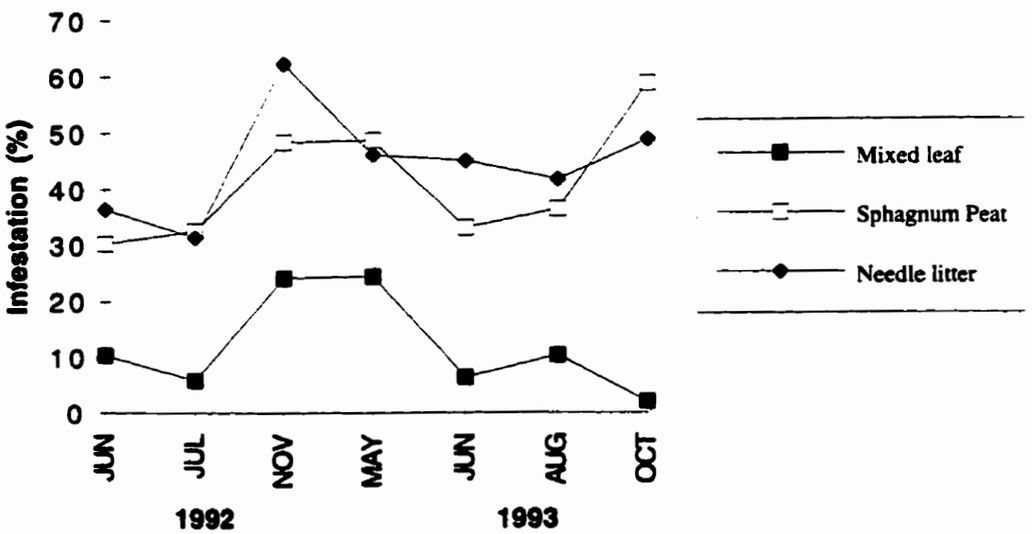

Fig. 5.6. Pollen infestations on seven sampling dates from three different litter types collected in the Mistik Creek study area.

infestations over the 88 sites and seven collecting dates for each of the chytrid taxa.) *Chytriomyces poculatus*, *P. papillatum*, and *R. sphaerotheca* showed seasonal high pollen infestations in spring and fall collections (Fig. 5.7). *Chytriomyces annulatus* pollen infestations are high from summer and fall collections concomitant with increased moisture and temperature in the study area (Fig. 5.2).

Pollen infestation levels for *Chytriomyces annulatus* and *C. poculatus* were higher in needle litter and sphagnum peat sites than in mixed leaf litter sites (Fig. 5.7). *Phlyctochytrium papillatum* and *Rhizophydium sphaerotheca* infested higher percentages of pollen bait in sphagnum peat collections than in needle litter or mixed leaf litter samples. Generally *C. annulatus* and *P. papillatum* infested pollen in plated needle litter and sphagnum peat collections, *C. poculatus* infested pollen added to needle litter, sphagnum peat and mixed leaf litter and *R. sphaerotheca* infested pollen with sphagnum peat and mixed leaf litter. Infestation levels by *C. annulatus* and *P. papillatum* were very low in mixed leaf litter microcosms and *R. sphaerotheca* infestations were low in needle litter plates.

A greater number of chytrid infestations occurred on pollen baited with needle litter collected in spring and fall than with needle litter collected during the summer (Fig. 5.7). High *Chytriomyces annulatus* infestations in summer collections are coupled with high levels of *C. poculatus* and *Phlyctochytrium papillatum* infestations with spring and fall samples. The same pattern is evidenced for peat with the added contribution of *Rhizophydium sphaerotheca* in the spring and fall collections. (From these four chytrid species, pollen infestations are almost always higher in samples of sphagnum peat than in needle

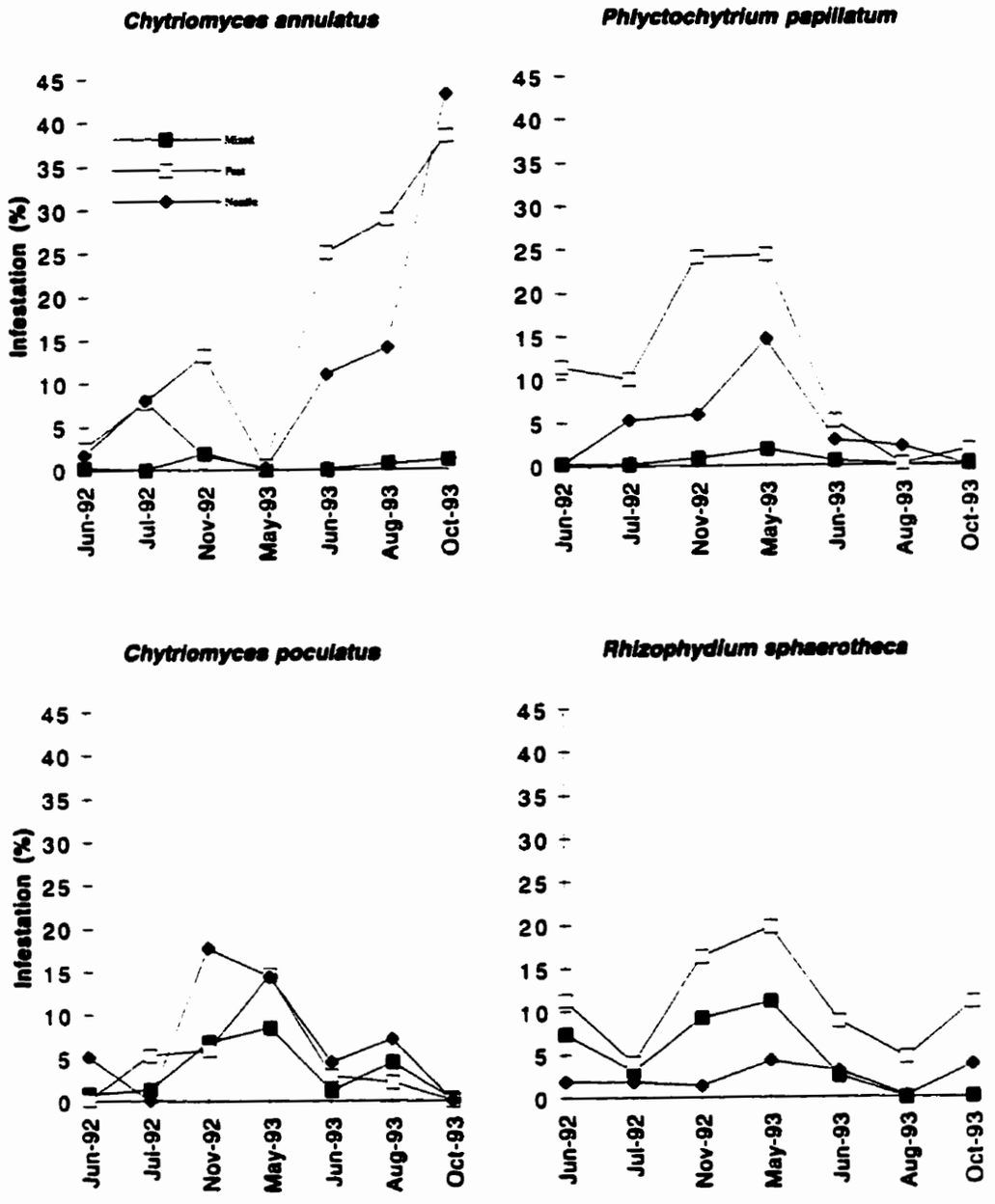

Fig. 5.7. Infestation percentages on seven sampling dates of four chytrid species from three different litter types in the Mistik Creek study area.

litter collections.) Pollen infestations in soils from mixed leaf litter by *C. poculatus* and *sphaerotheca* seem to be generally limited to the spring and fall.

DISCUSSION

In the Mistik Creek area, needle litter tends to predominate in the sites with drier soils and mixed or broad-leaf litter characterizes sites with moist soils. Needle litter of *Pinus banksiana* is reported to be highly acidic as compared with the pH of litter derived from other North American trees (Plice 1934). Decomposition of needle litter results in the formation of a soil with an accumulation of raw humus, a low base status and a low pH, while breakdown of broad leaf (angiospermous) litter tends to increase base content, improve buffering and decrease acidity (Millar 1974; Williams and Gray 1974; Read 1984). Broad leaf litter decomposes faster and, in initial stages, more thoroughly than needle litter (Hering 1982). Due to more rapid decomposition of angiospermous leaf litter, Mistik Creek region sites of broad leaf or mixed broad leaf and needle litter might be considered more ameliorated in chemical, thermal and moisture regimes than sites with a high level of coniferous needle litter.

The study area is composed of sites that range from open hotter ecoclimes over both drier and wetter soils to relatively closed, hotter, normal and cold ecoclimes over moist soil (Hills 1952). Soils in the study sites have mor profiles and are characterized by accumulation of litter in distinct organic layers. Further, these soils are relatively low in nitrogen (C:N ratio ~ 1:100), which, in these soils, is mostly in the form of indigestible phenolic-protein complexes (Hering 1982).

Infestations of pollen by chytrid species when placed with soils from the Mistik Creek study area are correlated with pH and types of litter. The highest levels of infestation were observed on pollen placed with soils from collecting sites in the range of pH 4.0 to 5.2 (generally needle litter) while lower infestations were found on pollen added to litter and soil from higher pH (5.5 to 6.7) sites (broad leaf litter). Results from my study suggest that chytrids are environmentally specific.

Among the chytrids encountered in the Mistik Creek study area, *Chytriomyces poculatus* was previously distinguished as characteristic of acidic situations in England and Australia (Willoughby 1965) and the High Arctic (Booth and Barrett 1976). *Chytriomyces annulatus* was described as a chytrid of acidic sites (Dogma 1969; Booth and Barrett 1976) and *Phlyctochytrium papillatum* was also collected from acidic locations (Sparrow 1952; Miller 1965a). In reference to these species, my results confirm that *C. annulatus* and *P. papillatum* are characteristic of acidic (needle litter) sites. *Chytriomyces poculatus*, however, unlike Willoughby's (1965) findings, infested pollen across a fairly wide range of pH (~ 3.9 to 6.1). (The reader may wish to consult Chapter IV for distributional evidence supporting environmental specificity of these chytrids in selected Mistik Creek study sites.)

Rhizophydium sphaerotheca, previously recovered from sites of pH 5.0 or less (Willoughby 1965), was also collected from both acidic and alkaline sites by workers (Gaertner 1954; Booth 1971c; Booth and Barrett 1976). In Mistik Creek boreal sites, the organism that I identified as *R. sphaerotheca* occurred over a wide range of pH (4.3 to 6.5). *Triparticalcar arcticum* (Barr) Barr, a chytrid infesting pollen added to soils and litter from cooler sites (Ellesmere Island and Devon Island, N.W.T. Canada) (Booth and Barrett 1971, 1976; Barr 1980) and

somewhat morphologically similar to *Phlyctochytrium reinboldtae*, occurred in alkaline and cooler moist soils. *Phlyctochytrium reinboldtae* was originally described from alkaline soil collections (Persiel 1959) and is generally considered a chytrid of higher pH environments (Booth 1971c). In my study area, however, it occurs in soils over a pH range of 5.6 to 6.6.

Gradients of environmental factors are a source of niche separation for pollen inhabiting chytrids and decomposing fungi in general. Environmental specificity (Swift 1982) is evidenced in my results by: i) higher pollen infestation in the more acidic sites, i.e. sphagnum peat and needle litter, for all epibiotic chytrids; ii) higher acidic sites pollen infestation by four selected chytrids, i.e. *Chytriomyces annulatus*, *C. poculatus*, *Rhizophydium sphaerotheca* and *Phlyctochytrium papillatum*; and iii) general occurrence of *C. annulatus* and *P. papillatum* in needle litter and sphagnum peat sites and *R. sphaerotheca* in peat and mixed leaf litter sites. (*Chytriomyces poculatus* is recorded from needle litter, sphagnum peat and mixed litter sites, suggesting that this taxon is not environmentally specific to these litter types.) Although environmental specificity for the distribution of chytrids in my study region is clearly affected by pH and soil types, a more thorough understanding of the niche of chytrids in the boreal forest requires consideration of resource (pollen) availability and specificity, interactions with other organisms and colonization strategies.

Over the 88 sites of this study, total pollen deposition ranged from 9 to 25.5 kg/ha/season. Such pollen rain represents a significant seasonal contribution of nutrients and substrates which may act as a "kick start" for microbial activity (Stark 1972; Hutchison and Barron 1997). Microbial activities contribute, by various processes, to the pool of nutrients available to forest trees in the spring and early summer. Inorganic and organic nitrogen, sufficient to contribute 336.5

g N/ha/season, is available in sporopollenin (carotinoid esters) and glycoproteins (bacula chambers) of the exine, protein of the intine and water insoluble molecules remaining within the grains. Among the other insoluble substrates found in pollen are cellulose in the primexine and intine as well as hemicellulose and pectin incorporated into the intine (Brett and Waldron 1996). These substrates are not only available to chytrids but also to decomposer basidiomycetes and ectomycorrhizal fungi.

It is known that chytrids play an important part in the decay of pollen under acidic conditions (Roberts 1963). Many wood-rotting fungi (lignicolous fungi) are mesothermic, with cardinal temperatures in the region of 5, 25 and 40°C (Wagner and Davidson 1954; Cartwright and Findlay 1958). The more mesic litter of deciduous forests is favourable to the development of a richer filamentous decomposer mycota and more active litter decomposition than in the drier litter of pure coniferous stands (Cooke 1979). In contrast, chytrids are reported to be present and capable of pollen infestation in relatively cold conditions (Booth and Barrett 1971, 1976). Infestation results from the Mistik Creek region also strongly suggest that pollen infesting chytrids are adapted to sites that are seasonally quite dry.

Additions of pollen to soils and litter are known to stimulate decomposition by filamentous fungi with a concomitant increase in hydrogen activity and probable reduction in bacterial competition for resource and associated substrates (Stark 1972). Hutchison and Barron (1997) demonstrated that a great number of lignicolous fungi are capable of directly exploiting pollen. Lignicolous fungi, many of which are decomposer basidiomycetes, procure carbon by producing degradative enzymes (Hering 1982). Likewise, chytrids exploit carbon from pollen through exoenzymatic action. Similarity in substrate procurement

mechanism and utilization of the same resource, suggest possible competitive interaction among chytrids, other fungal decomposers, and bacteria.

Resource competition between chytrids and decomposers, including decomposer basidiomycetes, evokes possibility of employment of an escaper strategy (Grime 1979; Pugh 1980; Rayner and Webber 1984) by chytrids. With the highest levels of pollen infestation in the Mistik Creek study sites occurring in open, hotter ecoclimes over both drier and wetter, acidic soils with needle litter, it is reasonable to conclude that the chytrids may escape competition from other pollen decomposers by inhabiting sites which are sub-optimal and hostile for other decomposers. Evidence most directly supporting this conclusion involves hydrogen ion activity in litter and soil, thermal regimes and soil moisture amelioration. It is well known that many potential decomposer organisms are inactive or less active when the pH is below 5.0 (Millar 1974; Boddy 1992). As moisture and temperature regimes are time dependent in Manitoba's boreal, this suggests temporal separation of chytrids and possible competitors.

Phenological data showing pollen infestations by the four selected chytrids over the litter types strongly suggests temporal separation of their infestation periods. Swift (1982) considers such temporal separation a colonization strategy. Combining environmental specificity and temporal separation (specificity), as descriptive of the complex of factors delineating realized niche, obviates more broadly defined characterization of the colonization strategies of the chytrids studied. *Chytriomyces annulatus*, *Phlyctochytrium papillatum* and *Rhizophydium sphaerotheca* all demonstrate environmental and temporal specificity. *Chytriomyces annulatus* and *P. papillatum* are specific to the same environmental type (acidic) but are temporally separated. *Rhizophydium sphaerotheca* is specific to environments of ameliorated moisture regimes.

Temporal specificity describes the colonization strategy of the widely distributed *Chytriomyces poculatus* which, in terms of litter types, does not exhibit environmental specificity.

As organisms colonizing a resistant resource generally unavailable to members of other groups, with the exception of lignicolous fungi (Hutchison and Barron 1997), chytrids may be characterized more specifically as survivors/escapers (Pugh 1980). *Chytriomyces poculatus*, *Phlyctochytrium papillatum* and *Rhizophydium sphaerotheca*, zymogenous organisms (Winogradsky 1924), primarily infesting pollen in spring and fall collections, seem to escape the optimal period (summer) for growth of filamentous decomposers (Wagner and Davidson 1954; Cartwright and Findlay 1958), thereby escaping competition. The equally zymogenous *Chytriomyces annulatus*, with generally high levels of pollen infestation in the summer, may be ecologically identified as a ruderal (Pugh 1980) or perhaps more fully, a competitive ruderal (Booth et al. 1988).

Ultimately, these strategies suggest that pollen in needle litter and sphagnum peat sites is infested under conditions of sufficient moisture by chytrids over the entire decomposition period, i.e., spring, summer and fall. In mixed leaf litter sites pollen is infested primarily in the spring and fall. It is reported that in warm, moisture ameliorated broad leaf litter lignicolous fungal growth and concomitant decomposition activities are optimal (Williams and Gray 1974; Hering 1982; Read 1984). It might be assumed that during their period of peak activity (summer) these active lignicolous fungi, some of which are known to infest pollen, limit chytrid access to the pollen resource (Stark 1972, 1973; Hutchison and Barron 1997).

Chapter VI
General Discussion

Deposition of Macronutrients by Pollen

Pollen studies show that significant amounts of important elements are delivered to the temperate forest floor by pollen (Stark 1972; Doskey and Ugoagwu 1989). Pollen grains raining on the forest floor are broken down within two months (Stark 1972), suggesting that pollen may be an important source of macronutrients during the critical early summer growth period. By comparison, the mean turnover rate of leaf litter in the pine forests of boreal North America is about 10 years (Prescott et al. 1989) and seasonal litter fall profoundly affects litter-inhabiting fungi (Hintikka 1982; Mitchell 1982). Because pollen grains are rapidly decomposed and are high in nutrients, pollen rain may be an important component of nutrient dynamics in terrestrial and aquatic ecosystems. Despite this fact, pollen generally has been overlooked in studies of forest nutrient cycling .

As early as the 1930's, researchers showed the nutritional and stimulatory value of pollen to fungal growth (Bransvheidt 1930; Schopfer 1934). Stark (1972, 1973) reports that pine pollen enhances decomposition by providing an early-summer macronutrient pulse to decomposers in the litter fermentation zone. The cytoplasm of pollen grains is rich in vitamins, carbohydrates, lipids, amino acids, and proteins (Faegri 1971; Stanley and Linskens 1974). Stark (1973) reports that after the spring pollen rain, the fermentation zone shows an increase in nitrogen and phosphorus. Bonan and Van Cleve (1992) show that increased N mineralization in the black spruce soil stimulates tree growth. Competition for

nitrogen may occur in substrates of high C/N ratio such as woody plant residues (Lockwood 1992). Nitrogen is present in mor soils under conifers in large amounts but, in contrast to mull soils, a high proportion is usually unavailable for plant growth (Millar 1974).

In northern Wisconsin, a significant proportion of the annual atmospheric deposition of phosphorus (20%) and potassium (45%) is attributable to pollen (Doskey and Ugoagwu 1989). In 30-year, jack pine stands of northern Ontario phosphorus and nitrogen are limited due to low rates of litter decomposition (Foster and Morrison 1976). In these stands, annual per ha nutrient uptake rates are estimated at 26 kg N, 1.7 kg P, and 15.2 kg K. Corresponding values for nutrient deposition by pollen (Yellow Leg regenerating jack pine stand) are 0.5 kg N, 0.07 kg P, and 0.20 kg K, suggesting that pollen contributes relatively little to overall stand nutrient dynamics. However, rapid turnover rate of pollen nutrients combined with episodic deposition suggest that pollen may play a disproportionate role in boreal forest nutrient cycling, even though nutrient contributions by pollen are small when contrasted to nutrients in litter fall (Stark 1972; Foster and Morrison 1976).

Annual deposition of jack pine pollen averages 7.7 to 9.0 kg/ha (total pollen 16.1 kg/ha) along the mixed forest transect, and 19.6 to 24.6 kg/ha in two regenerating jack pine stands in the Mistik Creek study area, corresponding to nutrient inputs of 0.34 to 0.49 kg N/ha, 0.04 to 0.07 kg P/ha, and 0.11 to 0.20 kg K/ha. These values are greater than the 0.9-3.0 kg/ha range reported for Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) stands in Nevada (Stark 1972), but fall within the broad 3.5-80.0 kg/ha range estimated for white (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) stands in northern Wisconsin (Doskey and Ugoagwu 1989). Although the amounts of each element added to the boreal forest floor is

not likely to be significant to tree growth directly, they are of a magnitude to be of value to microorganisms in the forest soil. (Though the amounts of these nutrients are limited, it is logical to assume that at least some of them are taken up by plants and their associated mycotrophs.)

Pollen and Environmental Specificity

Various workers (Remy 1948; Willoughby 1964, 1965; Booth 1971c; Booth and Barrett 1976) report that higher levels of pollen infestation by chytrids occur in soils rich in organic matter and lower infestation levels occur in mineral or soils lacking organic matter. Pollen infestation is affected by types of decaying litter and high rates of infestation are generally characteristic of litter with high needle content, whereas medium infestations occur in mixed (needle and broad leaf) litter. Baited collections from sites with mineral soil or soil with limited organic matter demonstrate low levels of pollen infestation. It is possible that types of litter can affect occurrence of chytrid and intensity of infestation through amount of available water, concentration of organic matter and exchangeable cation content.

Pollen infestations by chytrid species in the Mistik Creek study area are related to pH and litter types along a gradient of sites. The highest levels of infestation, taken to represent maximum pollen utilization, are observed from collecting sites (generally needle litter) in the range of pH 4.0 to 5.2 while lower infestations are evidenced on pollen added to litter and soil from higher pH (5.5 to 6.7) sites (broad leaf litter). Mistik Creek pollen infestation along the 88 sites results suggest chytrid environmental specificity. Perhaps, as with certain other factors of environment, the capacity to live and thrive under such low conditions

of pH may confer a definite competitive advantage to chytrids that escape competition for the pollen.

Colonization Strategies and Interactions

Pollen utilization by chytrids, decomposers and ectomycorrhizal fungi involves interactions among individuals and groups of organisms exploiting the resource. Resource exploitation may be neutralistic, mutualistic or competitive (Cooke and Rayner 1984; Rayner and Webber 1984). The role of litter inhabiting chytrids in the Mistik Creek study area reflects interactions with other organisms and colonization strategies. Chytrids probably have roles in initial colonization and degradation of resistant pollen substrate in boreal forests, thereby making it less refractory for other microbes and plants.

Considering competitive interactions between chytrids, environmental specificity combined with temporal specificity suggest that these zymogenous organisms may be escapers/survivors or competitive ruderals (Pugh 1980). Realized niches of *Chytriomyces annulatus* Dogma, *C. poculatus* Willoughby and Townley, *Rhizophydium sphaerotheca* Zopf (sensu Booth) and *Phlyctochytrium papillatum* Sparrow result in pollen infestation over spring, summer and fall needle litter and sphagnum peat collections and spring and fall mixed leaf litter samples from the Mistik Creek study region.

Ectomycorrhizal fungi in the Mistik Creek study region are also seasonal in peak activity as observed by others (Wu et al. 1993). These fungi may use the water soluble macronutrients of pollen as well as the nitrogen mobilized by chytrids. Chytrid spores may release nitrogen on death and it is observed that in freshly harvested zoospores (*Blastocladiella emersonii* Cantino & Hyatt) proteins make up ≈ 60% of by dry weight and total cell nitrogen is 5.4 pg/spore

(Suberkropp and Cantino 1973). Nitrogen available in one jack pine pollen grain is sufficient to produce 400 zoospores. Spore dissemination, cell lysis and cell membrane disruption presents a possible mechanism of nitrogen mobilization. Coincident pollen availability, chytrid infestation and formation of ectomycorrhizas (Appendix VII, this dissertation) circumstantially suggest a possible link between pollen breakdown and mycotrophic uptake (Appendix VIII, this dissertation).

Future Research

The identified complexity of interactions involving pollen decomposers, including chytrids, and ectomycorrhizal fungi suggests a series of specific questions aimed at further understanding the role of pollen in the boreal forest. These questions, based on the circumstantial evidence presented in my dissertation encompass the identified fungal exploiters of the resource (pollen) and pollen macronutrients, substrates and decomposition products.

1. What are the pollen substrates being exploited by pollen decomposers and infestors?
2. What are the decomposition products of pollen?
3. What competitive interactions occur between chytrids and other pollen decomposers and how do they operate?
4. Do the products of pollen decomposition stimulate to ectomycorrhizal fungi?
5. What are the steps and mechanisms for the flow of nutrients from pollen into trees?
6. What organisms are capable of mobilizing pollen nutrients?
7. What are the evidences and processes for mutualistic interactions between chytrids and ectomycorrhizal fungi?

8. Are fungi, chytrids and invertebrate pollen utilizers linked in providing nutrients to boreal forest trees?
9. Can pollen nutrients directly stimulate young coniferous seedlings?
10. What is the ecological value of coniferous tree (chiefly jack pine) allocation to excessive pollen productions in terms of species maintenance?

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APPENDIX I

Site Descriptions of 88 Sites

(* most common tree species at each site; + next common tree species)

Site	Canopy trees	Tall trees and others	Forest floor	Canopy height	Forest soil	Site characteristics
1R (1,2)	*Picea glauca* +*Populus tremuloides*	*Abies balsamea* *Alnus crispa*	Fallen trees and lichens	15-22m	Deep, dry, undecayed organic matter	On the lake shore ridge
1L (3,4)	**Populus tremuloides* +*Picea glauca*	*Abies balsamea* *Alnus crispa*	Fallen trees and lichens	15-22m	Deep, dry,undecayed organic matter	On the lake shore ridge
2R (5,6)	**Picea glauca* +*Populus tremuloides* *P. balsamifera*	*Abies balsamea* *Alnus crispa* *Ledum groenlandicum*	Fallen trees, mosses and grasses	15-20m	Deep, dry,undecayed organic matter	On the lake shore ridge
2L (7,8)	**Picea glauca* +*Populus tremuloides*	*Abies balsamea* *Alnus crispa* *Ledum groenlandicum*	Fallen trees and Lichens	15-20m	Deep, dry, and undecayed organic matter	On the lake shore ridge, steep
3R (9,10)	**Picea glauca* +*P. mariana* *Populus tremuloides*	*Abies balsamea* *Alnus crispa* Sapling of *P. mariana* and *P. tremuloides*	Grasses and open patch	15-32m	Dry sandy or loam	On the lake shore, open disturbed
3L (11,12)	**Picea glauca* +*P. mariana* *Pinus banksiana*	*Abies balsamea* *Alnus crispa*	Herbs and open patches	15-20m	Loam or sandy soil, dry	On the lake shore, disturbed
4R (13,14)	**Picea mariana* +*Populus tremuloides*	*Alnus crispa*	Fallen trees and herbs	10-15m	Deep and dry-mesic	On the lake plain
4L (15,16)	**Picea mariana* +*Populus tremuloides* *Picea glauca* *Pinus banksiana*	*Alnus crispa* Sapling of *Abies balsamea*	Grasses and open	15-20m	Deep and dry	On the lake plain
5R (17,18)	**Pinus banksiana* +*Picea mariana*	*Alnus crispa*	Grasses, lichens, open	15m	Sandy and dry	On sandy plain
5L (19,20)	**Pinus banksiana* +*Picea mariana* *Populus tremuloides*	*Alnus crispa*	Bare sand, open	15m	Sandy and dry	On sandy plain
6R (21,22)	**Picea mariana* +*Populus tremuloides* *Pinus banksiana*	*Alnus crispa* *Cornus canadensis*	Fallen trees, thick litter layer, open	15-18m	Deep and dry	Near highway No.10 corner
6L (23,24)	**Populus tremuloides* +*Pinus banksiana* *Picea mariana*	*Alnus crispa* *Salix* sp.	Herbs, open patches	12-15m	Sandy and dry	Open disturbed near highway No.10 corner
7R (25,26)	**Populus tremuloides* +*Picea mariana*	*Alnus rugosa* *A. crispa* *Salix* sp.	Lichens, herbs	10-12m	Shallow and mesic	On the ridge

7L (27,28)	**Picea mariana* +*Populus tremuloides* *Pinus banksiana*	*Alnus crispa*	Fallen trees, lichens, some open bare sites	10-12m	Loam or sandy, mesic	Disturbed by Right-of-way, low land
8R (29,30)	**Picea mariana* +*Pinus banksiana*	*Alnus crispa* *Salix* sp.	Lichens, mosses, open	8-12m	Shallow, dry-mesic-wet	Pine on the rock, spruce on the low land
8L (31,32)	**Pinus banksiana* +*Picea mariana*	*Alnus crispa* *A. rugosa* *Salix* sp.	Herbs,open	10-12m	Shallow on the rock, dry-mesic	On open rock ridge
9R (33,34)	**Populus balsamea* +*Betula papyrifera* *Populus tremuloides*	*Alnus rugosa* *A.crispa* *Salix* sp.	*Carex*, lichens, open	8-10m	Shallow, mesic	On the low land, ridge edge
9L (35,36)	**Picea mariana*	*Salix* sp. *Alnus crispa* *A. rugosa*	Mosses, grasses,dense shrubs	10-12m	Bog, mosses, mesic-wet	Low land, bog site
10R (37,38)	**Picea mariana* +*Pinus banksiana*	*Alnus crispa* *Salix* sp.	Lichens, open	10m	Shallow, dry	On the uphill ridge
10L (39,40)	**Picea mariana* +*Populus tremuloides* *Pinus banksiana*	*Salix* sp. *Alnus crispa* *A. rugosa*	Lichens, grasses	10-12m	Shallow,dry-mesic	On the ridge, down to lowland backside
11R (41,42)	**Pinus banksiana* +*Picea mariana* *Populus balsamifera*	*Alnus crispa* *Salix* sp.	Some bare patches, grasses	5-10m	Shallow, dry	On the downhill ridge
11L (43,44)	**Picea mariana*	*Salix* sp.	Mosses, *Carex*	10-14m	Dry bog, mosses, mesic	Lowland
12R (45,46)	**Picea mariana* +*P. glauca* *Populus balsamifera*	*Alnus rugosa* *Salix* sp. *Larix laricina*	Grasses	12-18m	Deep, dry	On creek shore, downhill
12L (47,48)	**Picea glauca* +*P. mariana* *Betula papyrifera*	*Alnus crispa* *Salix* sp.	Mosses, open	12-18m	Deep, dry	Lowland
13R (49,50)	**Picea mariana* +*Larix laricina*	*Alnus crispa* *Betula papyrifera* *Salix* sp.	Mosses, open	5-8m	Wet bog, mosses	Open bog, distubed
13L (51,52)	**Picea mariana*	*Alnus rugosa* *Betula papyrifera*	Mosses, *Carex*	10-13m	Dry bog, mosses, mesic	Low land
14R (53,54)	**Picea mariana* +*Pinus banksiana*	*Alnus crispa* *Betula papyrifera* *Larix larciana*	Lichens, bare rock patches	7-12m	Shallow on the rock bed, dry-mesic	On the rock ridge, down to lowland
14L (55,56)	**Picea mariana* +*Pinus banksiana*	*Alnus crispa* *Salix* sp.	Lichens, grasses, bare rock patches	7-12m	Shallow on the rock bed, dry	On the rock ridge, down to lowland

15R (57,58)	*Betula papyrifera* +*Pinus banksiana* *Picea mariana*	*Alnus crispa*	*Carex*, undecayed litter layer	3-10m	Loam, *Carex*, mesic	Low open land, disturbed, small water paddy
15L (59,60)	**Picea mariana* +*Betula papyrifera*	*Alnus rugosa* *Salix* sp. *Alnus crispa*	*Carex*, mosses	10-12m	*Carex*, mosses, mesic-wet	Low open bog land
16R (61,62)	**Picea mariana*	*Salix* sp. *Alnus crispa*	Mosses, *Carex*, open	10-14m	Mosses, *Carex*, mesic	Low dry land
16L (63,64)	**Picea mariana* +*Larix laricina* *Betula papyrifera*	*Alnus crispa* *A. rugosa* *Salix* sp.	*Carex*, mosses, closed	7-10m	*Carex*, mosses, mesic	Low land
17R (65,66)	**Picea mariana*	*Salix* sp. *Betula papyrifera* *Larix laricina*	Mosses	5-10m	Mosses, mesic-wet	Low bog land
17L (67,68)	**Picea mariana* +*Larix laricina*	*Alnus crispa* *Salix* sp.	Mosses, shrubs, closed	7-12m	Mosses, mesic-wet	Low bog land
18R (69,70)	**Pinus banksiana* +*Picea mariana*	*Alnus crispa*	Lichens, shrubs, open	5-12m	Shallow on the rock bed, dry	On the rock ridge down to lowland
18L (71,72)	**Picea mariana*	*Alnus crispa* *Salix* sp.	Shrubs, *Carex*, open	7-10m	*Carex*, dry-mesic	On the downward lowland, disturbed
19R (73,74)	**Picea mariana* +*Pinus banksiana* *Larix laricina*	*Salix* sp. *Alnus crispa* *A. rugosa*	Lichens, shrubs, open	8-12m	Shallow on the rock bed, dry-mesic	On the rock ridge down to lowland
19L (75,76)	**Picea mariana* +*Larix laricina*	*Salix* sp. *Alnus crispa* *A. rugosa*	Mosses, *Carex*, open	7-10m	Mosses, *Carex*, mesic	Low open bog
20R (77,78)	**Picea mariana* +*Populus tremuloides* *Pinus banksiana*	*Alnus crispa*	Lichens, grasses, open	8-12m	Shallow on the rock bed, dry	On the rock ridge beside small pond
20L (79,80)	**Picea mariana*	*Alnus rugosa* *Salix* sp.	Mosses, *Carex*, shrubs	7-10m	Mosses, mesic-wet	Low land bog
21R (81,82)	**Picea mariana* +*Pinus banksiana*	*Alnus crispa*	Lichens, grasses, open	8-12m	Shallow on the rock bed, dry	On the rock ridge open, near creek
21L (83,84)	**Populus tremuloides* +*Pinus banksiana*	*Alnus crispa* *Populus balsamifera* *Salix* sp.	Grasses, Rosa sp. open patches	3-6m	Loam or sandy, dry	Disturbed open plain, near creek
22R (85,86)	**Picea mariana* +*Pinus banksiana*	*Populus balsamifera* *P. tremuloides* *Salix* sp.	Lichens, fallen trees	10-15m	Shallow on the rock bed, dry	On the uphill ridge
22L (87,88)	**Picea mariana* +*Pinus banksiana*	*Populus tremuloides*	Fallen trees, lichens, simple	10-15m	Shallow on the rock bed, dry	On the uphill ridge

APPENDIX II

Vegetation Data

(Abbreviations for species name: AB = *Abies balsamea*; AC = *Alnus crispa*; AG = *Alnus rugosa*; BP = *Betula papyrifera*; JP = *Pinus banksiana*; LL = *Larix laricina*; PB = *Polulus balsamifera*; PG = *Picea glauca*; PM = *Picea mariana*; PT = *Populus tremuloides*; SA = *Salix* spp.)

Site	Species	No. of trees	Rela. density (%)	Total basal area (cm^2)	Rela. dominance (%)	Rela. frequncy (%)	Importance Index	Ave. basal area/tree (cm^2)	Trees /ha	Basal area /ha (m^2)
1R	AC	2	5	27	0.2	3.7	8.9			
(1,2)	BP	2	5	183	1.3	7.4	13.7			
	AB	12	30	717	5.1	25.9	61			
	PT	8	20	3873	27.7	22.2	69.9	350	3543	124
	PM	4	10	408	2.9	14.8	27.7			
	PG	12	30	8779	62.8	25.9	118.7			
1L	AC	9	22.5	117	1.1	23.1	46.7			
(3,4)	BP	1	2.5	121	1.1	3.8	7.4			
	AB	8	20	611	5.5	15.4	40.9			
	PT	9	22.5	5720	51.6	23.1	97.2	277	2403	67
	PM	5	12.5	267	2.4	15.4	30.3			
	PG	8	20	4258	38.4	19.2	77.6			
2R	AC	6	15	112	0.7	16	31.7			
(5,6)	PB	5	12.5	3886	0.9	12	27.9			
	AB	6	15	140	23.7	8	44.2			
	PT	6	15	4015	24.5	16	55.5	410	2099	86
	PM	4	10	435	2.7	4	28.7			
	PG	12	30	7812	47.6	16	105.6			
	SA	1	2.5	11	0.1	28	6.6			
2L	AC	5	12.5	78	1.1	8.3	21.9			
(7,8)	BP	1	2.5	8	0.1	4.2	6.8			
	AB	3	7.5	177	2.5	8.3	18.3			
	PT	15	37.5	2673	37.3	33.3	108.1	179	2236	40
	PM	5	12.5	324	4.5	12.5	29.5			
	PG	11	27.5	3898	54.5	33.3	115.3			
3R	AC	5	12.5	92	1.7	17.4	31.6			
(9,10)	AB	1	2.5	16	0.3	4.3	7.1			
	PB	1	2.5	8	0.1	4.3	6.9			
	PT	9	22.5	887	16.4	17.4	56.3	135	2800	38
	PM	14	35	1358	25.2	30.4	90.6			
	PG	9	22.5	2867	53.1	21.7	97.3			
	JP	1	2.5	168	3.1	4.3	9.9			
3L	AC	4	10	59	1	16.7	27.7			
(11,12)	AB	2	5	34	0.6	8.3	13.9			
	PT	1	2.5	127	2.2	4.2	8.9			
	PM	18	45	1075	19	37.5	101.5	141	2029	29
	PG	14	35	3073	54.4	29.2	118.6			
	JP	1	2.5	1284	22.7	4.2	29.4			
4R	AC	7	17.5	98	2.4	28.6	48.5			
(13,14)	PT	7	17.5	151	3.7	23.8	45	103	2107	22
	PM	26	65	3865	93.9	47.6	206.5			
4L	AC	7	17.5	102	1.9	20	39.4			
(15,16)	AB	3	7.5	32	0.6	12	20.1			
	PT	8	20	1293	24.4	24	68.4	133	3061	41
	PM	20	50	1756	33.1	36	119.1			
	PG	2	5	2126	40	8	53			
5R	AC	4	10	49	1	25	36			
(17,18)	PT	1	2.5	215	4.2	6.3	13			
	PM	21	52.5	1252	24.6	37.5	114.6	127	2822	36
	JP	14	35	3570	70.2	31.2	136.4			
5L	AC	10	25	92	2.2	22.7	49.9			
(19,20)	PT	4	10	467	11	13.6	34.6			
	SA	1	2.5	10	0.1	4.5	7.1	106	5828	62
	PM	7	17.5	108	2.6	18.2	38.3			
	JP	18	45	3556	84	40.9	169.9			
6R	AC	8	20	91	1.8	23.8	45.6			
(21,22)	PT	11	27.5	1975	38.6	28.6	94.7			
	PM	20	50	2457	48.1	42.9	141	128	3341	43
	JP	1	2.5	589	11.5	4.8	18.8			

6L	AC	8	20	108	2.4	22.7	45.1			
(23,24)	BP	1	2.5	11	0.2	4.5	7.2			
	PT	15	37.5	2090	45.9	27.3	110.7			
	SA	2	5	36	0.8	9.1	14.9	114	2829	32
	PM	8	20	575	12.6	22.7	55.3			
	JP	6	15	1729	38	13.6	66.6			
7R	AC	2	5	18	0.6	4.5	10.1			
(25,26)	AR	7	17.5	102	3.2	22.7	43.4			
	PB	1	2.5	2	0.1	4.5	7.1			
	PT	13	32.5	1497	46.9	36.4	115.8	80	3586	29
	SA	3	7.5	30	0.9	4.5	12.9			
	PM	14	35	1541	48.3	27.3	110.6			
7L	AC	2	5	19	0.8	10.5	16.3			
(27,28)	BP	1	2.5	29	1.3	5.3	9.1			
	PT	12	30	1000	44.5	26.3	100.8	56	3618	20
	SA	2	5	24	1.1	5.3	11.4			
	PM	21	52.5	968	43.1	42.1	137.7			
	JP	2	5	207	9.2	10.5	24.7			
8R	AC	3	7.5	27	0.9	15.8	24.2			
(29,30)	BP	1	2.5	8	0.1	5.3	7.9			
	PT	2	5	140	4.9	5.3	15.2	71	2762	20
	SA	8	20	97	3.4	15.8	39.2			
	PM	17	42.5	1070	37.5	36.8	116.8			
	JP	9	22.5	1518	53.2	21.1	96.8			
8L	AC	5	12.5	43	1.2	16.7	30.4			
(31,32)	AR	3	7.5	43	1.2	11.1	19.8			
	SA	1	2.5	11	3.4	11.1	19.5	90	3846	35
	PT	2	5	122	0.3	5.6	8.4			
	PM	15	37.5	929	25.8	27.8	91.1			
	JP	14	35	2449	68.1	27.8	130.9			
9R	AC	4	10	44	1.4	10.3	21.7			
(33,34)	AR	6	15	113	3.7	13.8	32.5			
	BP	7	17.5	787	25.8	13.8	57.1			
	PB	9	22.5	916	30	20.7	73.2	76	4627	35
	PT	8	20	152	5	20.7	45.7			
	SA	2	5	24	0.8	6.9	12.7			
	PM	3	7.5	223	7.3	10.3	25.1			
	PG	1	2.5	796	26.1	3.4	32			
9L	AC	4	10	38	1.3	15	26.3			
(35,36)	AR	3	7.5	56	1.9	15	24.4			
	BP	2	5	73	2.5	10	17.5	72	6080	44
	SA	8	20	99	3.4	20	43.4			
	PM	23	57.5	2612	90.8	40	188.3			
10R	AC	1	2.5	11	0.4	5.3	8.2			
(37,38)	PT	2	5	29	1.1	10.5	16.6			
	SA	1	2.5	8	0.3	5.3	8.1	63	2532	16
	PM	30	75	1155	45.7	52.6	173.3			
	JP	6	15	1327	52.5	26.3	93.8			
10L	AC	7	17.5	82	4.1	15.8	37.4			
(39,40)	AR	3	7.5	39	2	5.3	14.8			
	PT	3	7.5	336	16.9	10.5	34.9	50	3104	16
	SA	6	15	84	4.2	26.3	45.5			
	PM	20	50	978	49.1	36.8	135.9			
	JP	1	2.5	472	23.7	5.3	31.5			
11R	AC	6	15	54	3.2	17.4	35.6			
(41,42)	BP	3	7.5	24	1.4	8.7	17.6			
	PB	4	10	24	1.4	13	24.4			
	PT	1	2.5	23	1.4	4.3	8.2	42	6636	28
	SA	4	10	58	3.4	8.7	22.1			
	PM	13	32.5	512	30.3	26.1	88.9			
	JP	9	22.5	994	58.9	21.7	103.1			
11L	SA	5	12.5	45	1.5	23.1	37.1	73	6324	46
(43,44)	PM	35	87.5	2867	98.5	76.9	262.9			

12R (45,46)	AC	3	7.5	40	1.6	11.1	20.2			
	BP	4	10	29	1.2	11.1	22.3			
	PB	4	10	37	1.5	16.7	28.2			
	LL	1	2.5	13	0.5	5.6	8.6	62	5308	33
	SA	4	10	32	1.3	11.1	22.4			
	PM	23	57.5	1272	51	38.9	147.4			
	PG	1	2.5	1070	42.9	5.6	51			
12L (47,48)	AC	2	5	16	0.5	3.7	9.2			
	AR	11	27.5	130	3.7	22.2	53.4			
	BP	5	12.5	486	13.7	14.8	41			
	PB	3	7.5	24	0.7	7.4	15.6	88	4612	41
	PT	3	7.5	29	0.8	11.1	19.4			
	SA	6	15	82	2.3	11.1	32.1			
	PM	8	20	308	8.7	22.2	50.9			
	PG	2	5	2462	69.6	3.7	78.3			
13R (49,50)	AC	9	22.5	94	5.5	25	53			
	BP	2	5	89	5.2	10	20.2			
	LL	14	35	728	42.2	25	102.2	43	3256	14
	SA	1	2.5	8	0.5	5	8			
	PM	14	35	805	46.7	35	116.7			
13L (51,52)	AR	5	12.5	60	6	13.3	31.8			
	BP	6	15	28	2.8	20	37.8	25	3931	10
	PT	1	2.5	32	3.2	6.7	12.4			
	PM	28	70	872	87.9	60	217.9			
14R (53,54)	AC	10	25	98	13.5	18.5	57			
	BP	6	15	56	7.7	14.8	37.5			
	PT	1	2.5	10	1.4	3.7	7.6			
	LL	2	5	33	4.6	7.4	17	18	3139	6
	SA	3	7.5	30	4.1	11.1	22.7			
	PM	11	27.5	255	35.2	29.6	92.3			
	JP	7	17.5	243	33.5	14.8	65.8			
14L (55.56)	AC	4	10	38	1.8	22.2	34			
	SA	1	2.5	8	0.4	5.6	8.5	52	2986	16
	PM	31	77.5	1282	62.1	55.6	195.2			
	JP	4	10	737	35.7	16.7	62.4			
15R (57,58)	AC	12	30	155	18.8	30.4	79.2			
	BP	10	25	196	23.7	21.7	70.4			
	PT	2	5	34	4.1	4.3	13.4			
	LL	1	2.5	8	1	4.3	7.8	21	2006	4
	SA	5	12.5	55	6.7	13	32.2			
	PM	6	15	157	19	13	47			
	JP	4	10	221	26.8	13	49.8			
15L (59,60)	AC	2	5	19	0.9	11.8	17.7			
	AR	3	7.5	54	2.5	11.8	21.8			
	BP	2	5	664	31.3	11.8	48.1	53	7496	40
	SA	5	12.5	57	2.7	11.8	27			
	PM	26	65	1075	50.7	47.1	162.8			
	JP	2	5	253	11.9	5.9	22.8			
16R (61,62)	AC	1	2.5	5	0.3	8.3	11.1			
	SA	1	2.5	8	0.5	8.3	11.3	43	4941	21
	PM	38	95	1708	99.2	83.3	277.5			
16L (63,64)	AC	9	22.5	90	5	17.4	44.9			
	AR	6	15	82	4.6	17.4	37			
	BP	7	17.5	339	19	13	49.5	45	5612	25
	LL	5	12.5	448	25.1	13	50.6			
	SA	3	7.5	27	1.5	13	22			
	PM	10	25	800	44.8	26.1	95.9			
17R (65,66)	BP	1	2.5	115	10.1	7.1	19.7			
	LL	1	2.5	109	9.5	7.1	19.1	29	5507	16
	SA	2	5	13	1.1	14.3	20.4			
	PM	36	90	907	79.3	71.4	240.7			

17L	AC	9	22.5	66	8.4	25	55.9			
(67,68)	PB	1	2.5	23	2.9	5	10.4			
	LL	4	10	33	4.2	15	29.2	20	2194	4
	SA	2	5	16	2	10	17			
	PM	24	60	644	82.4	45	187.4			
18R	AC	14	35	156	11.3	26.1	72.4			
(69,70)	AR	1	2.5	20	1.5	4.3	8.3			
	BP	1	2.5	18	1.3	4.3	8.1			
	PB	3	7.5	34	2.5	8.7	18.7	34	4272	15
	PT	2	5	96	7	8.7	20.7			
	PM	10	25	365	26.5	21.7	73.2			
	JP	9	22.5	689	50	26.1	98.6			
18L	AC	2	5	22	1.5	7.7	14.2			
(71,72)	LL	1	2.5	18	1.2	7.7	11.4	38	2322	9
	PM	36	90	1363	90.5	76.9	257.4			
	JP	1	2.5	103	6.8	7.7	17			
19R	AC	5	12.5	46	3.8	15	31.3			
(73,74)	AR	12	30	252	21	20	71			
	BP	3	7.5	31	2.6	10	20.1			
	PT	1	2.5	72	6	5	13.5	30	2962	9
	LL	1	2.5	11	0.9	5	8.4			
	PM	14	35	528	43.9	30	108.9			
	JP	4	10	264	21.9	15	46.9			
19L	AC	1	2.5	11	0.6	5.3	8.4			
(75,76)	AR	1	2.5	8	0.4	5.3	8.2			
	SA	3	7.5	32	1.7	10.5	19.7	48	6400	31
	LL	5	12.5	572	29.8	21.1	63.4			
	PM	29	72.5	1241	64.7	52.6	189.8			
	JP	1	2.5	54	2.8	5.3	10.6			
20R	AC	6	15	85	2.7	16.7	34.4			
(77,78)	PB	2	5	193	6.2	11.1	22.3			
	PT	12	30	508	16.4	27.8	74.2	78	3717	29
	PM	17	42.5	1338	43.1	27.8	113.4			
	JP	3	7.5	977	31.5	16.7	55.7			
20L	AR	13	32.5	179	8.1	35	75.6			
(79,80)	BP	2	5	41	1.8	5	11.8	56	5288	29
	SA	6	15	98	4.4	25	44.4			
	PM	19	47.5	1905	85.7	35	168.2			
21R	AC	6	15	48	1.6	10.5	27.1			
(81,82)	PT	2	5	16	0.5	10.5	16	76	2179	17
	PM	22	55	1498	49.4	47.4	151.8			
	JP	10	25	1470	48.5	31.6	105.1			
21L	AC	11	27.5	80	18.1	24.1	69.7			
(83,84)	PB	9	22.5	97	21.9	27.6	72			
	PT	10	25	96	21.7	17.2	63.9	11	726	0.8
	SA	8	20	82	18.6	24.1	62.7			
	JP	2	5	87	19.7	6.9	31.6			
22R	PB	4	10	62	1.4	10	21.4			
(85,86)	PT	2	5	27	0.6	10	15.6			
	SA	1	2.5	2	0.1	5	7.6	115	2284	26
	PM	21	55	1990	42.8	45	143.4			
	JP	12	27.5	2499	55.2	30	112.1			
22L	PT	3	7.5	174	3.2	7.5	28.3			
(87,88)	PM	29	72.5	2638	47.8	72.5	179.1	138	2664	37
	JP	8	20	2708	49.1	20	92.5			

APPENDIX III

Pollen Data
(1991-1993)

(grains/cm^2/48 hrs, except 1991 Jack pine pollen - 24 hrs)

1991 Jack pine pollen

Date /Site	Site-1	Site-2	Site-3	Site-4	Site-5	Site-6	Site-7	Site-8	Site-9	Site-10	Site-11	Site-12	Site-13	Mean	Stdev
31-May-91	97	290	137	233	138	92	195	98	98	85	113	102	63	134	66
1-Jun-91	564	1658	791	1321	783	519	1104	574	557	481	642	575	359	764	376
2-Jun-91	766	2187	1066	1743	1443	788	2109	877	988	589	944	1044	922	1189	518
3-Jun-91	1066	3430	1410	2986	1377	988	1820	1088	944	899	1232	910	311	1420	871
4-Jun-91	311	833	477	500	344	289	578	300	300	433	367	333	156	401	169
5-Jun-91	155	422	311	422	144	122	156	89	122	122	167	144	133	193	114
6-Jun-91	167	183	106	128	78	117	111	167	117	100	111	131	125	126	30
7-Jun-91	78	206	111	111	86	69	120	114	67	56	89	128	114	104	38
8-Jun-91	22	67	28	59	56	28	45	17	11	16	19	25	22	32	18
9-Jun-91	22	25	28	45	22	14	39	31	28	9	25	22	36	26	10
10-Jun-91	16	16	14	36	11	20	28	11	14	6	20	14	14	17	8
11-Jun-91	31	53	45	95	14	45	17	6	30	17	53	28	11	34	24
12-Jun-91	14	17	11	9	28	9	6	9	14	3	11	9	3	11	7
13-Jun-91	8	20	3	11	6	3	6	8	3	9	3	6	9	7	5
14-Jun-91	14	6	17	6	16	3	14	3	3	3	6	6	16	9	6
15-Jun-91	6	14	6	9	11	9	6	3	6	3	3	3	11	7	4
16-Jun-91	3	9	6	3	3	0	0	0	3	3	3	0	9	3	3
17-Jun-91	3	11	3	6	9	6	6	0	0	3	0	3	3	4	3
Sum	3327	9429	4552	7719	4567	3117	6356	3379	3302	2835	3806	3481	2315	4476	2105

1992 Jack pine pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2
6-7JUNE92	5	5	10	5	5	5	10	0	0	0	0	0	0	0	0	0	0	0	0	5	10	0	5	5
8-9JUNE92	367	288	332	327	304	241	262	354	370	393	314	212	299	275	362	291	566	582	629	540	576	409	563	375
10-11JUNE92	975	700	936	877	605	570	613	846	869	944	747	516	841	826	935	790	1951	1659	1647	1392	1518	1203	1408	849
12-13JUNE92	1337	1022	1298	963	1082	1002	884	1298	1297	1710	924	1023	1711	1416	1710	1376	2949	2556	1770	2163	2065	2123	1868	2300
14-15JUNE92	256	275	315	452	334	295	374	374	609	177	236	216	275	334	374	452	904	1042	708	727	295	472	708	570
16-17JUNE92	492	354	413	570	433	433	295	492	472	688	374	452	629	315	609	452	708	924	786	1022	865	668	668	924
18-19JUNE92	106	100	154	130	106	118	94	106	189	154	112	106	165	100	236	200	313	265	242	171	224	163	236	224
20-21JUNE92	53	50	77	65	53	59	47	53	95	77	56	53	83	50	118	100	156	133	121	86	112	92	118	112
22-23JUNE92	18	17	26	22	18	20	16	18	32	26	19	18	28	17	39	33	52	44	40	29	37	31	39	37
SUM	3609	2811	3560	3410	2940	2743	2595	3541	3932	4168	2782	2598	4030	3333	4383	3695	7599	7205	5943	6134	5703	5180	5813	5397

Date / Site	7R1	7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2
6-7JUNE92	0	0	0	0	10	0	0	10	0	0	0	0	0	0	0	0	0	0	0	10	20	30	0	0
8-9JUNE92	409	456	488	370	435	346	637	506	448	511	393	519	574	543	480	511	480	496	252	207	397	289	440	401
10-11JUNE92	1222	1156	1203	751	1246	952	1918	1785	1066	1317	1003	1290	1529	2151	1269	2084	1211	1549	593	590	782	684	1133	1172
12-13JUNE92	1160	1730	1533	1160	1455	1258	1769	2339	1317	1592	1199	1592	2084	2162	1022	2929	1749	2575	1710	1160	1278	1180	1495	1376
14-15JUNE92	550	315	492	295	236	334	609	570	275	472	295	256	433	413	197	413	452	413	197	354	492	374	374	413
16-17JUNE92	413	727	668	629	511	354	688	727	472	629	668	609	688	649	845	688	511	629	550	708	570	609	472	806
18-19JUNE92	189	236	100	83	177	118	165	171	148	159	100	106	183	159	154	177	165	206	88	260	124	171	112	171
20-21JUNE92	95	118	50	41	89	59	83	86	74	80	50	53	92	80	77	89	83	103	44	130	62	86	56	86
22-23JUNE92	32	39	17	14	30	20	28	29	25	27	17	18	31	27	26	30	28	34	15	43	21	29	19	29
SUM	4089	4777	4551	3343	4188	3441	5896	6222	3824	4786	3725	4443	5613	6183	4069	6920	4678	6006	3449	3462	3745	3451	4101	4453

Date / Site	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2
6-7JUNE92	0	10	0	0	0	0	89	20	10	10	0	0	15	0	0	0	0	0	0	0	30	10	20	0
8-9JUNE92	124	324	425	378	472	370	513	617	293	395	244	236	306	370	314	228	378	362	378	417	612	388	334	322
10-11JUNE92	362	806	873	959	1160	1104	1227	1722	1093	1620	680	983	928	1065	905	558	1058	817	1175	920	1659	1510	865	936
12-13JUNE92	1258	1022	1082	1435	2379	1553	2045	2221	1927	2418	1199	1003	1200	1710	1061	1061	1376	1475	1809	924	2064	1770	1180	1612
14-15JUNE92	295	256	452	374	374	374	629	413	236	413	216	177	236	354	275	295	256	236	413	334	511	492	275	393
16-17JUNE92	629	452	629	590	629	826	865	865	668	806	511	590	649	433	550	708	433	393	433	393	649	865	492	649
18-19JUNE92	88	59	212	159	165	165	519	224	183	165	154	136	136	206	165	165	248	307	136	171	136	242	124	65
20-21JUNE92	44	29	106	80	83	83	260	112	92	83	77	68	68	103	83	83	124	153	68	86	68	121	62	32
22-23JUNE92	15	10	35	27	28	28	87	37	31	28	26	23	23	34	28	28	41	51	23	29	23	40	21	11
SUM	2815	2968	3815	4001	5289	4502	6233	6232	4532	5937	3106	3215	3560	4276	3380	3125	3914	3794	4434	3273	5750	5438	3371	4020

Date / Site	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
6-7JUNE92	0	20	0	10	30	20	10	0	10	0	10	59	10	10	0	0	6	13
8-9JUNE92	417	358	496	403	572	413	293	260	568	543	435	562	710	616	590	637	415	122
10-11JUNE92	1234	1136	1313	1160	1699	1180	799	1018	1723	1777	1502	1876	2131	1911	1888	1859	1171	423
12-13JUNE92	1986	1986	1652	1691	2595	1789	1494	1887	1631	1966	3047	3146	2261	2123	2202	2930	1680	548
14-15JUNE92	472	511	334	354	1180	845	334	315	550	727	550	609	865	649	609	688	430	194
16-17JUNE92	747	806	374	492	570	609	354	609	688	727	708	865	492	609	649	767	609	159
18-19JUNE92	242	118	124	112	254	224	148	88	336	336	218	177	319	307	165	194	176	73
20-21JUNE92	121	59	62	56	127	112	74	44	168	168	109	89	159	153	83	97	88	37
22-23JUNE92	40	20	21	19	42	37	25	15	56	56	36	30	53	51	28	32	29	12
SUM	5259	5013	4375	4297	7069	5229	3530	4236	5730	6300	6616	7412	7000	6429	6213	7205	4604	1315

1992 Spruce pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2
27-28MAY92	11	0	6	6	6	0	6	0	17	6	6	6	6	6	6	0	6	11	6	0	6	11	6	6	0	11	6	0	6	0
29-30MAY92	17	6	6	11	17	6	6	11	6	6	11	6	6	0	11	11	6	0	0	0	0	0	0	0	0	0	0	0	22	0
31MAY1JUNE92	324	393	305	285	305	374	393	472	492	315	334	334	167	69	423	383	147	147	128	88	20	118	187	69	79	79	89	79	197	118
2-3JUNE92	83	31	41	22	37	26	26	10	18	20	28	28	8	10	18	26	6	2	2	4	4	8	4	6	26	14	8	4	16	8
4-5JUNE92	165	63	82	43	75	51	51	20	35	39	55	55	16	20	35	51	12	4	4	8	8	16	8	12	51	28	16	8	32	16
6-7JUNE92	332	136	279	161	232	233	179	74	143	138	296	188	227	202	207	194	159	152	53	97	146	85	57	81	71	116	183	57	160	94
8-9JUNE92	423	300	443	384	404	487	453	113	442	502	654	398	1028	880	949	890	806	846	697	590	a36	689	541	453	374	452	619	433	561	570
10-11JUNE92	295	305	364	345	325	325	325	59	393	482	452	325	855	777	875	767	718	718	746	561	757	738	512	443	452	482	511	423	472	551
12-13JUNE92	197	99	118	197	59	157	255	295	217	177	79	216	315	118	256	314	197	236	177	236	197	255	295	197	315	236	98	197	99	138
14-15JUNE92	20	20	39	20	20	59	20	20	177	59	39	0	79	79	39	59	59	79	59	0	0	39	79	0	79	0	39	20	79	59
16-17JUNE92	79	98	59	59	138	157	20	79	20	79	98	20	197	39	20	20	79	118	98	59	118	138	98	98	79	138	20	59	138	98
18-19JUNE92	17	12	23	6	35	35	17	29	59	41	41	29	77	47	29	53	41	17	23	12	41	35	47	29	41	65	6	53	41	23
20-21JUNE92	9	6	12	3	18	18	9	15	29	21	21	15	38	24	15	26	21	9	12	6	21	18	24	15	21	32	3	26	21	12
22-23JUNE92	3	2	4	1	6	6	3	5	10	7	7	5	13	8	5	9	7	3	4	2	7	6	8	5	7	11	1	9	7	4
SUM	1974	1471	1781	1542	1677	1933	1762	1201	2058	1891	2121	1624	3031	2278	2887	2802	2263	2341	2009	1662	2160	2154	1865	1412	1594	1663	1578	1367	1849	1690

Date / Site	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2
27-28MAY92	6	6	0	0	6	6	6	17	6	11	22	6	6	6	0	0	11	6	6	0	6	6	0	11	22	0	6	0	11	11
29-30MAY92	0	0	0	6	0	6	0	0	0	0	0	0	0	0	0	6	6	6	6	0	0	0	0	0	0	0	0	0	0	0
31MAY1JUNE92	49	79	138	59	98	79	116	59	108	478	167	138	88	59	88	79	79	98	88	20	88	39	69	59	69	49	79	59	98	59
2-3JUNE92	10	2	18	18	10	0	18	6	8	26	14	2	2	6	2	6	8	2	4	4	26	0	8	4	0	8	4	16	0	0
4-5JUNE92	20	4	35	35	20	0	35	12	16	51	28	4	4	12	4	12	16	4	8	8	51	0	16	8	0	16	8	32	0	0
6-7JUNE92	197	181	114	134	89	69	94	199	75	120	136	83	63	110	44	71	114	73	28	48	159	177	153	57	10	114	57	120	59	40
8-9JUNE92	492	728	383	541	374	502	482	669	492	443	531	649	649	502	482	452	580	521	364	276	570	541	649	403	600	551	521	502	669	561
10-11JUNE92	354	571	325	482	384	472	482	521	453	413	462	668	688	482	581	472	561	590	423	315	501	482	570	374	649	590	511	413	649	600
12-13JUNE92	118	177	177	256	217	335	196	216	138	177	197	256	255	315	59	216	216	79	118	138	354	196	335	216	258	216	99	118	79	374
14-15JUNE92	59	39	39	39	0	0	20	20	39	20	20	59	0	59	59	20	0	39	39	79	0	0	59	39	59	39	20	79	39	59
16-17JUNE92	157	138	39	118	118	79	98	138	98	98	39	118	59	98	157	59	79	118	39	138	118	177	118	79	39	20	59	118	118	138
18-19JUNE92	35	35	23	35	35	53	12	53	29	35	17	29	23	108	53	35	17	53	35	23	41	47	29	29	94	41	12	12	12	35
20-21JUNE92	18	18	12	18	18	26	6	26	15	18	9	15	12	53	26	18	9	26	18	12	21	24	15	15	47	21	6	6	6	18
22-23JUNE92	6	6	4	6	6	9	2	9	5	6	3	5	4	18	9	6	3	9	6	4	7	8	5	5	16	7	2	2	2	6
SUM	1519	1983	1308	1746	1373	1635	1568	1943	1480	1895	1643	2031	1853	1825	1563	1451	1698	1624	1181	1084	1942	1698	2025	1299	1861	1671	1384	1476	1741	1900

Date / Site	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
27-28MAY92	6	11	6	28	17	0	11	11	6	6	6	6	0	22	6	6	6	6	6	0	11	6	11	6	11	0	6	6	7	6
29-30MAY92	0	6	0	0	0	6	12	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	6	0	0	3	5
31MAY1JUNE92	39	29	98	79	39	69	118	10	69	79	20	59	69	79	39	49	118	69	20	49	98	39	59	49	69	39	49	29	129	120
2-3JUNE92	4	8	2	10	14	22	14	0	12	4	8	8	16	8	8	10	8	6	10	2	2	6	2	2	10	14	6	0	11	12
4-5JUNE92	8	16	4	20	28	43	28	0	24	8	16	16	32	16	16	20	16	12	20	4	4	12	4	4	20	28	12	0	22	24
6-7JUNE92	57	104	73	98	97	92	87	108	83	126	75	94	110	45	65	49	94	110	69	63	132	81	73	53	118	67	41	99	114	62
8-9JUNE92	610	551	453	393	512	442	561	374	580	610	443	600	610	344	511	315	511	492	374	413	472	541	492	472	571	344	443	541	528	150
10-11JUNE92	659	482	443	354	463	413	640	345	541	512	423	541	551	335	560	364	531	413	345	452	403	551	443	521	531	364	433	482	494	140
12-13JUNE92	295	196	216	79	79	216	158	99	138	157	118	236	99	177	197	354	157	99	116	177	79	79	99	157	118	79	196	118	186	78
14-15JUNE92	20	0	39	20	59	39	59	0	39	20	98	39	59	0	59	39	59	98	59	20	20	20	0	59	39	59	39	59	40	30
16-17JUNE92	98	59	256	79	20	20	79	79	98	118	59	79	59	98	98	79	79	118	79	39	79	20	59	79	39	59	39	39	86	45
18-19JUNE92	47	6	29	47	17	29	41	35	17	41	41	41	17	12	35	0	17	12	12	17	35	17	23	17	23	12	23	35	32	18
20-21JUNE92	24	3	15	24	9	15	21	18	9	21	21	21	9	6	18	0	9	6	6	9	18	9	12	9	12	6	12	18	16	9
22-23JUNE92	8	1	5	8	3	5	7	6	3	7	7	7	3	2	6	0	3	2	2	3	6	3	4	3	4	2	4	6	5	3
SUM	1874	1471	1638	1238	1355	1411	1834	1090	1618	1708	1333	1746	1633	1143	1617	1284	1607	1442	1118	1248	1359	1383	1286	1430	1564	1078	1302	1431	1673	375

1992 Alder pollen (1)

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2
3-4MAY92	7	0	0	0	0	0	0	7	0	0	0	7	13	0	0	0	0	0	0	7	7	0	0	0
5-6MAY92	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0
7-8MAY92	6	0	6	0	0	6	11	22	0	0	0	0	0	6	0	0	0	0	0	0	0	6	0	0
9-10MAY92	0	0	0	0	0	0	0	0	0	0	6	6	11	0	6	11	0	6	6	6	6	0	22	11
11-12MAY92	0	0	0	0	0	0	0	0	11	6	0	0	0	6	0	0	0	0	0	0	0	0	0	0
13-14MAY92	0	0	0	0	6	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0
15-16MAY92	0	0	0	0	6	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
17-18MAY92	6	0	0	0	0	0	0	0	6	0	0	0	11	0	0	0	0	0	0	0	6	0	0	0
19-20MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0
21-22MAY92	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23-24MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25-26MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27-28MAY92	0	0	0	0	6	0	0	17	17	6	0	0	6	0	6	0	17	0	0	22	0	6	22	17
29-30MAY92	11	6	6	6	11	6	0	0	6	0	17	6	96	79	6	11	34	22	112	11	6	11	45	34
31MAY1JUNE92	20	20	0	0	0	10	49	59	59	39	59	49	609	423	20	98	10	29	1513	20	49	226	10	79
2-3JUNE92	0	0	0	0	0	0	0	0	0	0	10	0	20	20	0	0	0	10	20	10	0	10	0	0
4-5JUNE92	6	0	0	0	0	0	0	0	0	0	10	0	20	34	10	0	0	10	20	10	0	10	0	0
6-7JUNE92	23	10	0	0	11	0	0	0	11	10	79	10	245	310	59	29	10	29	324	49	10	39	0	10
8-9JUNE92	10	10	0	0	26	0	0	0	46	10	96	20	138	167	49	20	39	0	157	49	0	197	0	0
10-11JUNE92	0	10	0	10	0	0	0	0	0	0	0	0	200	59	39	0	20	0	96	49	0	39	0	0
12-13JUNE92	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0
SUM	95	56	12	26	75	22	66	105	158	71	279	96	1375	1104	195	169	130	112	2277	233	90	544	99	151

Date / Site	7R1	7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2
3-4MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	13	13	13	26	26	7	20	7	0
5-6MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	7	0	0
7-8MAY92	6	6	6	0	0	6	0	0	6	6	0	6	0	11	0	0	6	0	0	6	11	0	28	11
9-10MAY92	0	6	0	0	0	0	6	0	0	11	0	0	6	6	0	6	0	0	0	0	0	17	6	0
11-12MAY92	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
13-14MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
15-16MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17-18MAY92	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
19-20MAY92	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	6
21-22MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23-24MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
25-26MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
27-28MAY92	6	6	6	6	6	22	0	6	0	17	6	22	6	6	11	6	34	6	6	0	0	0	22	28
29-30MAY92	22	11	6	39	6	6	6	6	51	0	22	6	6	0	6	17	51	56	11	39	11	6	22	34
31MAY1JUNE92	79	59	20	69	0	49	0	10	20	20	10	0	20	10	29	49	79	157	10	10	29	10	0	275
2-3JUNE92	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	10	10
4-5JUNE92	0	0	0	10	20	0	0	10	10	0	0	0	0	0	0	0	0	10	0	0	0	0	10	10
6-7JUNE92	0	0	20	20	236	10	10	29	10	0	29	20	0	0	49	20	0	39	10	10	0	0	19	98
8-9JUNE92	0	0	0	20	59	10	0	0	10	10	49	0	0	0	10	0	0	0	0	0	0	0	0	69
10-11JUNE92	0	0	0	10	0	0	0	20	10	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12-13JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUM	125	88	58	174	347	103	22	81	123	93	116	54	38	33	112	117	189	291	70	91	64	66	141	541

1992 Alder pollen (2)

Date / Site	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2
3-4MAY92	20	46	13	46	0	7	26	33	7	7	111	7	7	20	46	131	0	0	0	0	26	13	0	7
5-6MAY92	0	0	13	0	0	0	7	0	0	7	7	7	0	0	26	7	0	0	0	0	0	0	0	0
7-8MAY92	0	6	17	0	6	17	0	6	6	0	6	11	0	6	17	28	0	0	0	0	0	0	0	0
9-10MAY92	0	0	6	6	0	0	0	6	0	6	17	0	0	0	79	22	0	0	0	0	0	0	0	0
11-12MAY92	0	0	17	0	0	0	0	0	0	0	0	17	0	28	0	17	0	0	0	0	0	0	0	0
13-14MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	6	0	6	0	0	0	0	0	0
15-16MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
17-18MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	6	17	11	0	0	0	0	0	6	0	0
19-20MAY92	0	6	0	6	0	0	0	0	0	0	6	0	0	0	22	0	0	0	0	0	0	0	0	0
21-22MAY92	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23-24MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25-26MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27-28MAY92	17	17	6	6	0	101	0	56	96	34	17	6	11	6	39	6	0	17	51	11	17	17	6	0
29-30MAY92	0	17	22	22	79	11	84	39	758	315	6	0	0	11	6	11	17	28	34	39	118	219	11	11
31MAY1JUNE92	39	10	39	29	20	88	157	10	816	393	29	20	0	0	20	49	39	29	423	29	79	147	10	10
2-3JUNE92	0	0	0	0	0	10	39	0	96	84	0	0	0	0	0	0	0	0	29	0	0	0	20	10
4-5JUNE92	0	0	0	0	0	10	10	10	157	84	10	0	0	0	0	0	0	0	39	10	10	0	0	0
6-7JUNE92	10	39	0	29	98	98	108	29	668	541	39	10	10	0	20	0	20	10	275	59	59	20	20	20
8-9JUNE92	0	0	0	0	118	0	98	0	56	304	10	0	0	0	10	0	10	0	157	39	0	0	0	0
10-11JUNE92	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	20	0	0	129	10	0	0	0	0
12-13JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0
SUM	86	141	133	144	321	342	569	189	2666	1775	258	78	28	77	319	308	86	90	1157	197	309	422	67	58

Date / Site	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
3-4MAY92	0	7	0	7	13	13	13	39	7	0	39	0	7	7	0	7	10	21
5-6MAY92	0	0	0	0	0	0	0	13	0	0	0	0	0	13	0	0	1	4
7-8MAY92	0	0	11	6	0	0	0	6	0	6	11	6	6	0	0	6	4	6
9-10MAY92	0	0	0	0	0	0	0	17	6	0	11	0	22	6	6	0	4	10
11-12MAY92	0	0	0	0	0	0	0	17	0	6	11	0	0	0	0	0	2	5
13-14MAY92	0	6	0	0	0	0	0	0	0	0	0	0	6	6	0	0	1	2
15-16MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
17-18MAY92	0	6	0	0	6	0	11	0	6	6	0	0	0	0	0	0	1	3
19-20MAY92	0	0	0	0	0	0	11	0	0	0	0	0	0	0	6	0	1	3
21-22MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
23-24MAY92	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25-26MAY92	0	0	0	0	0	0	0	0	0	0	17	6	0	6	0	0	0	2
27-28MAY92	0	17	0	6	22	22	6	22	0	0	302	263	28	11	17	0	18	44
29-30MAY92	34	45	11	6	84	51	6	0	11	56	152	893	6	0	6	34	48	129
31MAY1JUNE92	10	98	0	138	0	39	0	0	10	20	275	403	0	0	20	10	91	206
2-3JUNE92	29	45	0	0	0	10	0	0	0	10	10	152	0	10	0	0	8	22
4-5JUNE92	10	45	0	0	0	10	0	0	0	0	10	56	0	10	0	10	8	21
6-7JUNE92	59	138	10	10	0	69	10	0	0	39	39	541	20	20	29	10	58	120
8-9JUNE92	79	108	0	0	0	20	0	0	29	0	10	108	0	10	10	0	28	54
10-11JUNE92	0	0	0	0	0	0	0	0	10	0	0	39	0	29	0	0	10	29
12-13JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
SUM	221	515	38	173	125	234	57	114	79	143	887	2467	95	128	94	77	295	505

1992 Birch pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2
7-8MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9-10MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11-12MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13-14MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15-16MAY92	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17-18MAY92	0	0	6	6	17	6	6	17	0	6	0	6	11	6	0	0	0	6	6	0	6	6	6	6	0	22	6	6	0	6
19-20MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	6	0	0	0	0	0
21-22MAY92	0	0	0	6	0	0	0	0	0	0	0	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
23-24MAY92	22	17	6	0	17	6	6	6	11	11	0	17	0	0	0	0	11	17	11	0	6	11	17	11	22	0	0	0	6	0
25-26MAY92	39	22	34	45	39	51	28	67	28	28	17	39	6	34	22	34	11	17	28	6	11	11	6	6	6	11	28	51	28	17
27-28MAY92	28	28	22	6	22	22	6	45	34	17	17	17	17	11	6	39	45	28	17	17	22	11	0	11	17	6	6	11	28	28
29-30MAY92	0	0	6	0	11	6	11	6	0	6	0	6	17	0	6	0	11	0	6	0	6	6	0	67	11	6	6	0	0	0
31MAY1JUNE92	0	0	10	10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	10	0	20	0	0	0	20	0	10
2-3JUNE92	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0
4-5JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	10	0	0	0
6-7JUNE92	0	0	0	0	10	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0
SUM	89	67	84	73	116	91	67	141	83	74	34	91	67	51	34	73	78	68	68	23	61	55	49	117	62	45	82	68	72	61

Date / Site	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2
7-8MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9-10MAY92	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11-12MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0
13-14MAY92	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15-16MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17-18MAY92	0	11	0	11	0	11	6	11	11	0	0	0	0	0	0	6	6	6	0	0	6	0	0	6	6	0	0	22	0	0
19-20MAY92	0	0	6	6	0	6	0	0	0	0	0	6	0	0	0	0	11	0	0	0	0	0	11	0	11	0	34	0	0	6
21-22MAY92	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0
23-24MAY92	22	11	6	6	0	11	0	11	6	0	0	0	0	6	6	0	28	11	11	0	6	0	6	11	11	6	11	45	0	6
25-26MAY92	28	28	51	34	11	17	22	34	28	39	22	22	11	17	6	28	45	28	11	39	11	34	22	67	51	28	17	28	22	22
27-28MAY92	34	51	28	39	11	0	28	51	22	22	11	28	22	6	39	28	17	28	22	6	22	17	22	62	34	34	28	17	6	6
29-30MAY92	0	0	0	0	6	6	11	6	0	0	22	17	6	0	0	6	17	6	0	0	6	6	6	0	0	0	0	0	0	6
31MAY1JUNE92	0	10	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	10	0	0	10	0	0	10	0	10	0	0	0
2-3JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4-5JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
6-7JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUM	84	111	97	96	34	51	67	113	67	61	65	79	49	29	51	68	124	85	54	45	71	67	89	146	123	68	100	112	28	46

Date / Site	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
7-8MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	34	0	0	0.5	3.8
9-10MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.6
11-12MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	6	0	0	0.2	1.1
13-14MAY92	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	1.3
15-16MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.6
17-18MAY92	6	6	0	0	6	11	0	0	11	0	0	0	0	0	6	6	0	0	0	0	22	0	6	0	6	6	0	11	4.4	5.4
19-20MAY92	0	0	0	6	0	0	0	0	17	0	0	0	6	0	0	0	6	6	0	0	0	0	0	0	0	0	0	0	1.7	4.7
21-22MAY92	0	0	0	6	0	0	6	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0.9	2.9
23-24MAY92	0	17	6	0	6	0	17	0	11	17	0	0	6	17	6	11	6	6	0	0	11	6	6	6	6	6	6	6	7.4	7.7
25-26MAY92	39	28	11	34	22	11	28	6	11	11	34	6	28	39	17	0	39	28	28	34	17	34	34	22	28	51	17	22	25.8	13.9
27-28MAY92	28	17	34	45	17	11	11	28	11	28	11	22	11	22	34	28	6	28	11	17	6	34	22	28	28	17	11	17	21.7	12.3
29-30MAY92	0	0	0	0	0	0	0	0	17	11	6	0	0	0	0	0	0	0	6	0	0	6	0	0	11	6	0	0	4.4	8.4
31MAY1JUNE92	0	0	0	0	10	0	0	20	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.2	4.9
2-3JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	1.5
4-5JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	2.1
6-7JUNE92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	2.1
SUM	73	68	51	91	61	44	62	54	78	67	67	28	51	78	63	45	57	74	39	51	62	85	68	67	86	120	34	56	70.5	25.4

1992 Larch pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2
5-6MAY92	0	7	0	0	0	0	0	7	0	0	0	0	0	7	0	0	0	7	0	7	0	0	0	0	13	0	0	0	0	0
7-8MAY92	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0
9-10MAY92	0	0	0	0	0	6	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11-12MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
13-14MAY92	6	6	11	11	17	6	6	22	6	11	0	6	6	0	6	17	0	6	17	0	6	0	0	6	6	6	0	0	28	6
15-16MAY92	6	11	0	6	22	6	6	0	0	0	0	0	6	6	11	0	0	6	6	11	6	6	6	17	11	6	6	0	6	11
17-18MAY92	6	17	17	0	17	0	11	0	6	11	6	0	11	0	17	0	6	6	6	6	11	6	0	6	6	6	6	0	28	6
19-20MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0
21-22MAY92	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23-24MAY92	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25-26MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27-28MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60	0	0	0	0	0	0
SUM	18	47	34	17	56	24	23	29	12	22	6	6	29	13	34	17	12	25	29	24	23	12	6	95	47	18	12	0	62	23

Date / Site	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2
5-6MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7-8MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
9-10MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11-12MAY92	0	0	0	0	17	6	0	0	0	6	6	0	0	6	0	6	0	0	0	0	0	0	0	0	0	0	6	6	0	0
13-14MAY92	11	0	22	17	17	56	28	22	22	17	11	11	34	6	0	6	39	11	6	6	11	17	6	11	34	17	22	17	11	34
15-16MAY92	0	22	28	28	22	107	39	17	45	6	11	28	45	39	17	28	34	22	17	0	17	6	11	34	34	17	6	17	34	34
17-18MAY92	28	11	11	0	28	28	6	0	34	11	0	11	39	22	6	0	22	6	39	45	17	17	34	22	67	11	17	11	34	17
19-20MAY92	0	0	11	0	0	6	0	0	6	0	6	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21-22MAY92	0	6	11	0	0	0	0	0	0	0	0	6	0	0	6	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0
23-24MAY92	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
25-26MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
27-28MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	11	0	0	0	0	0	0	0	0
SUM	39	39	83	45	84	203	73	39	107	40	34	50	130	73	23	52	95	45	62	57	45	51	51	67	147	45	51	51	85	85

Date / Site	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
5-6MAY92	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	2.2
7-8MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	1.1
9-10MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0.2	1.1
11-12MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	6	0	0	0	0	0	0	0	0	0	0	0	6	0.9	2.6
13-14MAY92	56	39	45	39	11	28	11	17	39	22	6	28	22	6	17	22	11	11	45	6	6	17	11	6	11	6	6	17	14.8	12.8
15-16MAY92	67	45	39	73	73	34	22	17	39	22	45	39	11	45	28	34	11	11	51	45	45	11	17	17	11	11	0	6	20.6	19.7
17-18MAY92	51	22	45	17	34	34	62	6	45	22	39	28	17	17	28	22	0	11	51	34	6	17	11	11	17	6	17	11	17.0	15.1
19-20MAY92	0	0	22	0	6	6	0	0	11	0	0	0	0	6	6	6	0	0	0	0	0	0	0	0	0	0	0	0	1.2	3.5
21-22MAY92	0	0	6	0	0	0	0	0	0	11	6	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0.8	2.3
23-24MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0.3	1.3
25-26MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.6
27-28MAY92	0	0	0	6	0	0	0	0	0	0	6	6	0	0	0	6	0	0	0	0	0	6	0	0	0	0	0	0	1.2	6.6
SUM	174	106	157	135	124	102	95	40	141	77	102	101	50	80	79	96	22	33	159	85	63	51	39	34	39	23	23	40	57.9	42.6

1992 Poplar pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2
3-4MAY92	0	0	7	0	0	7	7	7	7	13	7	13	0	7	46	7	26	7	33	0	7	7	0	0	7	13	26	20	13	7
5-6MAY92	72	65	65	65	98	79	46	79	138	190	85	59	131	85	98	72	59	39	79	33	59	39	65	111	138	52	79	151	328	262
7-8MAY92	28	17	17	51	17	11	22	67	56	45	6	34	22	11	39	17	45	11	17	17	17	6	22	22	6	11	22	17	39	17
9-10MAY92	6	6	0	11	6	0	0	6	11	6	0	0	17	6	6	6	11	11	6	0	0	17	11	0	0	6	6	6	0	6
11-12MAY92	0	6	0	0	0	0	6	0	6	6	6	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0
13-14MAY92	6	0	6	11	0	0	0	0	0	6	0	0	0	0	0	0	0	0	6	0	0	0	0	28	0	0	0	0	0	0
15-16MAY92	17	6	0	17	22	6	6	11	11	6	11	11	6	0	0	0	0	0	0	0	11	0	0	28	6	0	11	0	0	11
17-18MAY92	45	51	34	22	62	22	22	22	6	17	11	17	6	6	11	11	11	11	6	11	11	11	0	6	56	39	11	45	34	34
19-20MAY92	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	110	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21-22MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0
SUM	174	151	129	177	205	125	109	192	235	289	126	145	182	115	200	223	152	79	147	61	105	80	98	201	213	127	155	239	414	337

Date / Site	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2
3-4MAY92	20	26	20	20	13	20	7	33	52	39	20	26	7	7	0	13	20	26	0	0	26	7	39	7	7	0	7	7	0	0
5-6MAY92	118	111	125	111	46	39	105	59	26	164	52	85	20	46	92	52	85	52	72	7	46	52	65	79	65	39	105	65	72	59
7-8MAY92	6	6	28	17	11	28	17	34	34	34	17	17	34	17	11	17	22	11	22	0	6	11	0	6	0	0	39	11	39	11
9-10MAY92	0	11	0	6	0	0	0	11	6	6	0	0	17	0	0	6	0	0	0	0	0	0	0	6	0	0	0	6	6	0
11-12MAY92	0	0	11	17	0	0	0	0	0	0	0	0	0	0	28	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
13-14MAY92	0	11	6	11	0	6	0	17	0	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
15-16MAY92	6	22	6	6	6	22	6	6	6	6	0	6	0	0	0	11	0	6	0	0	0	0	6	6	6	6	6	0	0	0
17-18MAY92	28	11	39	28	39	28	17	11	0	17	11	0	6	6	0	0	6	0	6	0	6	11	0	11	6	0	0	0	0	0
19-20MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21-22MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	6	0
SUM	178	198	235	216	115	143	152	171	124	272	106	134	84	82	137	99	139	101	100	7	84	81	110	115	84	45	163	89	123	70

Date / Site	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
3-4MAY92	0	0	20	7	7	0	0	7	7	0	0	0	13	7	7	7	26	20	7	7	0	7	7	13	0	0	7	13	11	11
5-6MAY92	13	13	26	39	59	33	20	26	79	98	46	59	85	46	33	13	105	65	59	26	13	65	85	85	26	111	26	26	73	50
7-8MAY92	17	0	34	45	28	11	6	6	17	17	11	11	6	17	6	6	34	45	6	6	6	28	6	0	6	0	0	6	18	14
9-10MAY92	0	0	11	0	0	0	0	0	0	11	0	0	0	6	6	0	11	6	0	6	22	0	6	0	0	6	6	0	4	5
11-12MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	6	0	0	0	0	0	0	0	0	0	0	1	4
13-14MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	6	2	4
15-16MAY92	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	11	6	6	6	6	0	0	6	0	0	17	5	6
17-18MAY92	0	0	6	11	11	6	0	0	11	0	6	0	6	6	11	0	6	6	0	6	0	0	11	6	11	0	0	0	12	14
19-20MAY92	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	12
21-22MAY92	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	1
SUM	30	13	97	102	105	50	32	45	114	132	63	70	110	99	63	26	188	159	78	57	47	112	115	104	49	117	39	68	128	71

1992 Willow pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2
3-4MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5-6MAY92	0	0	0	0	0	0	0	0	0	0	7	13	0	0	0	0	0	0	13	0	13	0	0	0	0	0	0	0	0	72
7-8MAY92	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9-10MAY92	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	6	6	0	0	0	0	0	0	0
11-12MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
13-14MAY92	0	0	6	6	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15-16MAY92	0	0	0	0	0	0	0	0	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17-18MAY92	0	0	0	0	11	6	0	6	6	6	0	0	0	0	6	0	0	0	6	0	0	0	0	0	0	11	0	0	0	6
19-20MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21-22MAY92	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23-24MAY92	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25-26MAY92	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27-28MAY92	0	6	0	0	0	6	0	0	6	0	0	6	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	6	0	0
29-30MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31MAY1JUN92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0
SUM	0	6	6	6	33	12	6	6	52	28	7	25	6	0	6	0	6	0	19	0	23	6	6	6	0	11	0	6	0	78

Date / Site	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2
3-4MAY92	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	7	0
5-6MAY92	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	13	0	0	7	0	0	7	0	0	0	0	0	0
7-8MAY92	34	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	6	0	0	6	0	0	0	0	0	0	6	0	0	0
9-10MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	17
11-12MAY92	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
13-14MAY92	0	0	0	22	0	6	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34
15-16MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17-18MAY92	0	0	6	22	0	0	0	0	6	0	0	0	11	0	0	6	0	6	0	0	0	0	0	0	0	0	0	11	0	0
19-20MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0
21-22MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23-24MAY92	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25-26MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
27-28MAY92	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29-30MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31MAY1JUN92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUM	34	0	13	50	0	6	7	17	12	0	6	0	11	0	0	6	6	19	0	6	7	6	0	7	0	6	6	35	13	51

Date / Site	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
3-4MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	7	0	0	7	0	0	0	0	0	0	0	0.5	2.1
5-6MAY92	0	0	0	0	7	20	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	13	7	0	13	7	0	2.6	8.6
7-8MAY92	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	4.6
9-10MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	6	0	0	0	0	0	0	0.6	2.3
11-12MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	6	0	0	0	0	0	0.4	1.7
13-14MAY92	0	0	0	0	22	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.3	5.0
15-16MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0.5	3.7
17-18MAY92	6	6	0	22	0	0	0	0	6	0	0	0	6	0	0	0	6	0	34	0	0	0	6	0	0	0	6	6	2.7	5.5
19-20MAY92	6	6	0	22	0	0	0	0	6	0	0	0	6	0	0	0	6	0	34	0	0	0	6	0	0	0	6	6	1.3	4.7
21-22MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.6
23-24MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.9
25-26MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0.4	2.5
27-28MAY92	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0.9	3.3
29-30MAY92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	79	0	0	0	0	0	0	0.9	8.4
31MAY1JUN92	0	0	0	0	0	0	0	0	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	3.3
SUM	23	12	0	44	51	26	0	0	41	7	0	0	12	0	7	0	29	7	68	12	7	91	37	7	0	13	19	12	13.7	18.4

1992 Total pollen

Species / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2
Pinus banksiana	3609	2811	3560	3410	2940	2743	2595	3541	3932	4166	2782	2596	4030	3333	4383	3695	7599	7205	5943	6134	5703	5180
Picea spp.	1974	1471	1781	1542	1677	1933	1762	1201	2058	1891	2121	1624	3031	2278	2887	2802	2263	2341	2009	1662	2160	2154
Alnus spp.	95	56	12	26	75	22	66	105	158	71	279	98	1375	1104	195	169	130	112	2277	233	90	544
Populus spp.	174	151	129	177	205	125	109	192	235	289	126	145	182	115	200	223	152	79	147	61	105	80
Betula papyrifera	89	67	84	73	116	91	67	141	83	74	34	91	67	51	34	73	78	68	68	23	61	55
Larix laricina	18	47	34	17	56	24	23	29	12	22	6	6	29	13	34	17	12	25	29	24	23	12
Salix spp.	0	6	6	6	33	12	6	6	52	26	7	25	6	0	6	0	6	0	19	0	23	6
SUM	5959	4609	5606	5251	5102	4950	4628	5215	6530	6543	5355	4585	8720	6894	7739	6979	10240	9830	10492	8137	8165	8031

Species / Site	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2
Pinus banksiana	5613	5397	4069	4777	4551	3343	4188	3441	5896	6222	3824	4786	3725	4443	5613	6183	4069	6920	4678	6006	3449	3462
Picea spp.	1865	1412	1594	1663	1578	1367	1849	1690	1519	1983	1306	1746	1373	1635	1568	1943	1480	1895	1643	2031	1853	1825
Alnus spp.	99	151	125	88	58	174	347	103	22	81	123	93	116	54	38	33	112	117	189	291	70	91
Populus spp.	98	201	213	127	155	239	414	337	178	198	235	216	115	143	152	171	124	272	106	134	84	82
Betula papyrifera	49	117	62	45	82	68	72	61	84	111	97	96	34	51	67	113	67	61	65	79	49	29
Larix laricina	6	95	47	18	12	0	62	23	39	39	83	45	84	203	73	39	107	40	34	50	130	73
Salix spp.	6	6	0	11	0	6	0	78	34	0	13	50	0	6	7	17	12	0	6	0	11	0
SUM	7736	7379	6110	6729	6436	5197	6932	5733	7772	8634	5681	7032	5447	6535	7518	8499	5971	9305	6721	8591	5646	5562

Species / Site	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2
Pinus banksiana	3745	3451	4101	4453	2815	2968	3815	4001	5289	4502	6233	6232	4532	5937	3106	3215	3560	4276	3380	3125	3914	3794
Picea spp.	1563	1451	1698	1624	1181	1064	1942	1696	2025	1299	1861	1671	1384	1476	1741	1900	1874	1471	1638	1238	1355	1411
Alnus spp.	64	66	141	541	86	141	133	144	321	342	569	189	2666	1775	258	78	28	77	319	308	86	90
Populus spp.	137	99	139	101	100	7	84	81	110	115	84	45	163	89	123	70	30	13	97	102	105	50
Betula papyrifera	51	68	124	85	54	45	71	67	89	146	123	68	100	112	28	46	73	68	51	91	61	44
Larix laricina	23	52	95	45	62	57	45	51	51	67	147	45	51	51	85	85	174	106	157	135	124	102
Salix spp.	0	6	6	19	0	6	7	6	0	7	0	6	6	35	13	51	23	12	0	44	51	26
SUM	5583	5193	6304	6868	4298	4288	6097	6046	7885	6478	9017	8256	8902	9475	5354	5445	5762	6023	5642	5043	5696	5517

Species / Site	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
Pinus banksiana	4434	3273	5750	5438	3371	4020	5259	5013	4375	4297	7069	5229	3530	4236	5730	6300	6616	7412	7000	6429	6213	7205
Picea spp.	1834	1090	1618	1708	1333	1746	1633	1143	1617	1284	1607	1442	1118	1248	1359	1383	1286	1430	1564	1078	1302	1431
Alnus spp.	1157	197	309	422	67	58	221	515	38	173	125	234	57	114	79	143	887	2467	95	128	94	77
Populus spp.	32	45	114	132	63	70	110	99	63	26	188	159	78	57	47	112	115	104	49	117	39	68
Betula papyrifera	62	54	78	67	67	28	51	78	63	45	57	74	39	51	62	85	68	67	86	120	34	56
Larix laricina	95	40	141	77	102	101	50	80	79	96	22	33	159	85	63	51	39	34	39	23	23	40
Salix spp.	0	0	41	7	0	0	12	0	7	0	29	7	68	12	7	91	37	7	0	13	19	12
SUM	7614	4699	8051	7851	5003	6023	7336	6928	6242	5921	9097	7178	5049	5803	7347	8165	9048	11521	8833	7908	7724	8889

1993 Jack pine pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2
1-2 JUNE 93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
3-4 JUNE 93	206	236	147	226	147	177	108	197	187	157	118	147	138	157	285	216	157	275	177	275	206	246	354	256
5-6 JUNE 93	157	138	157	138	197	118	79	177	236	334	98	98	216	138	374	236	767	963	649	570	433	354	590	983
7-8 JUNE 93	472	452	570	354	531	433	354	668	688	767	433	492	1042	885	806	806	3008	2654	2418	2045	1475	1455	2320	2693
9-10 JUNE 93	668	531	570	570	629	531	511	767	550	688	531	604	1298	708	826	1102	2359	2497	1887	1750	1278	885	1357	1180
11-12 JUNE 93	374	315	413	354	374	354	315	315	511	472	413	433	629	550	531	492	1003	924	747	708	786	590	747	845
13-14 JUNE 93	177	157	197	118	197	256	177	138	275	256	235	197	256	236	236	236	393	354	236	216	374	315	393	374
15-16 JUNE 93	108	108	98	98	88	98	69	138	147	128	98	69	128	108	128	206	216	197	167	147	147	138	177	79
17-18JUNE93	29	39	39	39	49	29	98	69	59	69	49	29	49	69	59	128	157	167	167	138	108	59	108	157
SUM	2191	1976	2191	1897	2212	1998	1711	2469	2653	2871	1975	2069	3756	2851	3251	3422	8060	8031	6448	5849	4807	4042	6046	6567

Date / Site	7R1	7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2
1-2 JUNE 93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3-4 JUNE 93	256	226	374	246	305	265	305	334	295	167	138	256	354	157	236	265	275	206	177	128	216	157	197	275
5-6 JUNE 93	177	315	334	236	393	334	511	826	197	275	275	295	531	550	393	236	256	629	236	197	256	157	295	197
7-8 JUNE 93	1022	1258	1317	944	1435	1199	1651	3067	1101	1121	924	1062	2615	3087	1946	2988	1337	1887	944	885	826	590	492	1081
9-10 JUNE 93	865	806	845	570	1258	983	1140	1848	1022	1022	727	1101	2163	2163	1573	1710	1966	1927	1062	1042	1180	1062	845	747
11-12 JUNE 93	570	550	472	433	472	786	511	767	492	629	472	452	983	924	747	865	786	747	374	570	649	256	354	334
13-14 JUNE 93	216	197	236	197	197	295	236	295	275	256	197	216	433	393	295	275	315	236	177	216	256	216	138	138
15-16 JUNE 93	128	118	138	108	118	128	147	206	128	147	157	157	177	187	138	138	138	177	157	108	88	69	118	98
17-18JUNE93	69	79	118	79	108	20	167	118	49	49	59	79	128	147	49	98	59	118	69	29	69	49	59	98
SUM	3303	3549	3834	2813	4286	4010	4668	7461	3559	3666	2949	3618	7364	7608	5377	6575	5132	5927	3196	3175	3540	2556	2498	2968

Date / Site	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2
1-2 JUNE 93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
3-4 JUNE 93	157	118	216	216	206	226	206	374	324	305	226	265	138	197	118	364	118	197	197	147	265	285	157	285
5-6 JUNE 93	157	118	197	275	197	256	315	236	315	393	334	334	216	295	413	374	393	334	354	374	374	590	334	275
7-8 JUNE 93	767	668	668	727	963	983	865	1671	944	1219	885	826	786	786	1062	1357	668	767	1140	747	1533	2458	786	1081
9-10 JUNE 93	786	786	845	845	1003	786	983	963	1160	1573	806	885	1062	826	472	727	727	806	963	413	1573	2418	1022	1160
11-12 JUNE 93	393	354	334	334	511	452	472	531	511	570	354	393	433	452	315	275	334	472	374	295	806	845	590	767
13-14 JUNE 93	197	216	138	138	216	157	197	256	236	197	138	157	197	256	177	177	138	177	197	118	315	354	216	295
15-16 JUNE 93	98	98	98	147	167	98	206	187	157	147	108	118	108	128	138	98	88	118	118	79	226	197	98	98
17-18JUNE93	79	59	98	69	98	49	79	128	59	69	108	69	49	69	69	59	88	59	79	29	98	118	98	69
SUM	2634	2417	2594	2751	3361	3007	3323	4346	3706	4473	2959	3047	2989	3009	2764	3431	2554	2930	3422	2202	5196	7265	3301	4030

Date / Site	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
1-2 JUNE 93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
3-4 JUNE 93	315	157	206	118	285	236	265	206	206	265	226	295	344	295	246	206	225	68
5-6 JUNE 93	433	354	315	334	315	295	236	295	550	511	531	511	413	433	472	354	342	178
7-8 JUNE 93	1612	1942	885	629	1750	1121	963	865	2575	1769	1612	1612	1907	1416	1769	1868	1264	696
9-10 JUNE 93	1258	1455	806	786	2497	1592	806	668	1573	1573	1396	1494	1180	1475	1278	1199	1120	498
11-12 JUNE 93	767	629	433	492	688	492	393	413	649	806	865	904	708	688	708	668	555	190
13-14 JUNE 93	334	256	197	256	315	216	197	177	295	275	531	531	531	295	315	295	247	88
15-16 JUNE 93	226	157	118	138	206	226	98	108	246	197	256	265	177	216	177	187	142	46
17-18JUNE93	98	69	39	59	88	128	69	59	128	157	147	118	118	118	138	128	85	36
SUM	5043	5019	2999	2812	6144	4306	3027	2791	6222	5553	5564	5730	5378	4936	5103	4905	3980	1803

1993 Spruce pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2
20-21MAY 93	10	0	0	0	20	0	0	10	0	30	10	10	0	0	0	10	0	10	0	0	29	10	0	0	0	10	0	0	0	0
22-23MAY 93	0	0	0	10	10	10	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	20	0	0	0	10	0	0	0	0
24-25MAY 93	39	20	20	0	49	0	20	20	10	29	0	10	29	10	20	29	10	10	0	0	59	69	10	0	0	0	0	10	0	0
26-27MAY 93	45	0	11	22	0	11	22	34	11	56	22	22	34	34	22	11	56	34	11	0	11	11	0	0	0	0	22	11	11	34
28-29MAY 93	17	22	22	101	39	73	67	56	51	51	67	79	67	107	84	67	11	45	11	28	28	34	17	0	73	56	17	45	62	84
30-31MAY 93	84	135	219	174	163	118	107	101	219	342	208	135	331	342	286	337	101	130	174	107	208	168	135	84	241	185	354	258	241	185
1-2JUNE 93	62	129	135	152	129	140	79	51	196	185	112	101	213	202	219	230	135	146	101	95	118	45	95	95	152	146	163	118	112	79
3-4JUNE 93	177	226	324	265	413	315	236	206	236	403	403	354	747	403	796	767	501	531	609	374	885	767	482	678	354	570	629	541	472	265
5-6JUNE 93	98	59	177	295	59	79	79	118	59	649	59	59	197	197	236	138	59	138	118	39	138	79	59	39	79	118	138	79	79	79
7-8JUNE 93	20	0	20	39	20	20	20	20	20	39	0	0	20	20	39	20	79	39	20	20	59	59	20	98	20	39	20	39	39	39
9-10JUNE 93	59	39	39	0	39	39	39	39	20	59	39	39	39	0	39	39	20	39	0	0	59	79	20	39	39	0	20	0	39	0
11-12JUNE 93	59	39	20	59	0	79	20	20	0	0	20	39	39	20	39	0	20	20	20	0	118	59	20	0	20	20	39	0	20	39
13-14JUNE 93	20	20	0	20	0	39	0	20	0	0	0	20	20	0	20	0	0	20	0	0	39	20	0	0	0	20	20	0	20	0
15-16JUNE 93	0	20	0	10	10	0	10	0	0	20	10	0	20	0	0	10	0	29	0	0	10	10	0	10	0	10	0	20	0	10
17-18JUNE 93	10	10	0	0	0	20	29	0	10	20	0	0	29	29	29	20	29	20	10	10	10	20	20	39	0	10	10	39	0	20
SUM	700	719	987	1147	951	943	728	695	832	1883	950	868	1785	1374	1829	1678	1021	1211	1074	673	1771	1450	878	1082	978	1194	1432	1160	1095	834

Date / Site	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2
20-21MAY 93	10	0	0	0	0	0	0	0	10	10	10	0	0	0	0	10	0	10	0	0	0	10	0	0	0	0	0	0	0	0
22-23MAY 93	0	0	0	0	0	0	10	0	20	0	0	0	0	0	0	0	0	0	0	0	0	20	0	10	0	0	10	0	10	0
24-25MAY 93	0	29	10	0	0	0	20	59	0	20	39	0	0	39	20	0	0	20	39	0	0	0	10	0	10	0	20	0	0	10
26-27MAY 93	11	11	11	11	0	11	90	0	45	11	0	22	0	11	0	11	0	11	22	0	0	22	11	11	0	0	34	22	0	11
28-29MAY 93	107	34	28	56	51	39	123	95	28	56	62	17	51	0	17	39	73	67	67	84	51	95	73	107	62	84	34	67	17	17
30-31MAY 93	219	236	84	79	67	123	129	174	135	118	84	90	79	101	168	174	118	112	129	219	185	230	275	219	140	140	118	168	118	90
1-2JUNE 93	118	135	84	79	67	129	146	185	135	118	84	90	79	101	168	185	118	112	118	146	101	135	163	112	129	112	84	129	112	84
3-4JUNE 93	413	442	364	531	364	413	560	482	452	560	590	383	659	629	364	442	393	364	383	393	531	855	442	354	501	511	560	413	541	442
5-6JUNE 93	118	79	79	39	39	39	59	39	39	59	79	39	39	177	118	177	79	59	79	59	118	197	79	39	118	59	79	59	79	59
7-8JUNE 93	79	20	20	39	20	39	39	59	20	39	39	0	20	0	59	39	0	59	59	79	98	138	39	39	59	20	39	20	39	20
9-10JUNE 93	98	59	39	0	0	59	59	20	20	20	20	79	39	20	39	39	20	0	39	39	79	20	0	20	39	0	0	0	39	20
11-12JUNE 93	0	0	20	39	59	39	59	20	59	20	0	39	20	20	20	0	20	0	20	20	39	20	59	79	39	20	0	39	20	20
13-14JUNE 93	0	0	0	0	20	0	20	20	20	0	0	0	0	20	0	0	0	0	0	20	0	20	39	39	0	20	0	0	0	20
15-16JUNE 93	10	10	20	0	0	0	20	10	20	20	0	0	0	0	39	0	10	20	0	10	10	10	0	20	20	0	0	0	0	0
17-18JUNE 93	0	0	0	20	0	0	20	10	0	20	20	0	20	29	10	0	0	10	39	0	0	0	10	0	20	10	10	20	0	0
SUM	1183	1055	759	893	687	891	1354	1173	1003	1071	1027	759	1008	1147	1022	1116	831	844	994	1069	1212	1772	1200	1049	1137	976	988	937	975	793

Date / Site	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
20-21MAY 93	0	0	0	0	10	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	20	10	0	0	0	0	10	0	3	6
22-23MAY 93	20	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	2	5
24-25MAY 93	0	0	0	20	0	0	0	20	20	20	0	0	39	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	11	16
26-27MAY 93	0	34	0	11	34	11	22	0	11	22	0	11	34	0	11	22	0	0	11	0	11	22	0	0	0	11	0	22	14	16
28-29MAY 93	51	62	45	34	112	67	90	45	67	62	39	62	39	84	34	17	67	51	45	73	39	28	45	34	28	56	67	73	53	27
30-31MAY 93	275	185	157	208	135	174	185	95	292	236	135	168	202	325	79	168	180	202	160	95	185	112	180	152	289	152	325	325	177	74
1-2JUNE 93	180	146	84	118	146	101	79	67	185	163	101	112	168	112	135	51	101	129	67	67	196	146	112	95	129	152	163	213	125	41
3-4JUNE 93	275	305	423	393	265	511	511	413	619	472	413	442	570	482	423	305	334	482	354	216	442	600	688	629	531	560	413	482	464	148
5-6JUNE 93	39	39	39	39	79	20	79	59	118	59	39	39	138	59	39	39	59	118	177	59	59	59	118	118	138	138	39	79	94	79
7-8JUNE 93	98	39	20	59	20	20	20	0	59	20	0	39	39	39	59	20	79	39	39	20	0	0	20	39	39	20	0	20	34	26
9-10JUNE 93	59	20	0	0	0	20	0	0	0	20	39	39	59	0	0	0	59	20	20	39	59	20	0	20	20	0	20	39	27	23
11-12JUNE 93	39	20	20	20	20	59	0	39	0	0	0	59	20	39	20	39	0	20	0	20	20	39	20	0	0	20	39	0	25	22
13-14JUNE 93	0	20	0	0	20	20	0	0	0	0	0	39	0	20	0	20	0	0	0	0	20	0	0	0	0	20	20	0	9	12
15-16JUNE 93	10	10	0	0	10	0	0	0	0	0	0	0	20	10	0	0	0	20	20	0	39	29	0	10	29	0	20	29	8	10
17-18JUNE 93	29	29	0	10	10	20	29	29	20	20	10	10	10	20	10	10	20	0	0	20	29	29	0	10	10	0	10	0	13	11
SUM	1075	909	788	912	861	1023	1015	767	1401	1104	776	1020	1338	1190	820	691	899	1081	913	609	1119	1094	1183	1107	1193	1129	1136	1282	1060	270

1993 Alder pollen

Date / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2
20-21MAY93	20	0	10	10	20	0	20	10	10	10	10	0	49	29	29	29	49	39	39	10	0	29	10	39	20	20	10	29	20	29
22-23MAY93	88	10	10	0	0	0	49	10	10	0	29	0	39	10	10	10	39	29	59	0	0	0	39	29	29	0	20	10	10	20
24-25MAY93	49	10	0	0	10	20	29	10	0	20	0	0	49	98	20	29	39	10	10	10	10	10	10	49	20	20	49	49	20	29
26-27MAY93	11	6	0	0	0	11	22	0	6	0	17	6	28	39	51	17	28	28	67	45	17	39	34	45	39	6	45	73	17	6
28-29MAY93	34	39	11	6	17	6	45	0	28	22	17	6	140	140	28	56	118	62	56	39	39	45	73	62	56	22	34	163	73	39
30-31MAY93	17	22	28	11	6	22	22	6	11	17	34	6	213	135	11	22	314	112	337	22	39	34	101	56	22	28	45	67	112	39
1-2JUNE93	6	6	6	17	0	0	28	11	0	6	95	22	135	168	17	34	34	202	185	17	51	28	22	17	11	34	28	34	51	6
3-4JUNE93	10	0	20	29	10	49	69	20	29	20	69	10	374	236	98	138	79	138	108	69	59	39	79	59	20	10	49	118	49	29
5-6JUNE93	0	0	0	0	0	0	0	0	0	0	0	0	216	98	20	20	59	0	20	0	0	59	10	10	0	0	20	0	20	0
7-8JUNE93	20	0	0	0	0	0	20	0	0	0	0	0	79	20	0	0	39	0	59	39	0	20	0	0	0	20	0	0	0	0
9-10JUNE93	0	0	0	0	0	0	0	0	20	0	0	0	79	59	20	0	40	0	20	0	0	0	0	0	0	0	0	0	20	0
11-12JUNE93	0	0	0	0	0	0	0	0	0	0	0	39	20	0	0	20	59	39	0	0	0	0	0	0	0	0	0	0	0	0
13-14JUNE93	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0
SUM	255	93	85	73	63	108	304	67	114	95	271	109	1421	1032	304	375	917	659	960	251	215	303	378	366	217	160	300	543	392	197

Date / Site	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2
20-21MAY93	20	29	0	29	20	20	0	20	10	10	39	49	20	49	0	0	10	20	0	0	20	0	49	10	29	20	49	29	20	0
22-23MAY93	10	0	0	20	0	10	0	20	0	10	0	10	0	0	10	0	0	39	0	0	0	0	0	0	10	10	79	29	0	10
24-25MAY93	20	0	10	29	10	0	10	49	0	0	59	69	10	0	0	0	0	59	0	0	29	0	10	10	0	10	29	79	0	10
26-27MAY93	11	6	51	56	0	6	6	17	0	6	95	17	28	11	6	11	22	17	6	6	17	17	45	17	11	6	56	73	11	0
28-29MAY93	28	6	17	34	0	10	17	22	11	34	135	34	34	28	22	22	51	51	17	17	22	28	28	22	17	11	123	107	0	0
30-31MAY93	34	0	34	56	11	17	22	17	0	11	112	67	67	28	17	11	45	17	28	39	6	17	84	22	45	17	292	213	6	17
1-2JUNE93	11	6	17	0	17	6	17	22	11	22	101	6	17	6	0	6	11	22	11	11	11	17	22	17	79	28	163	101	11	17
3-4JUNE93	39	10	29	49	0	39	10	68	29	39	49	29	88	59	10	49	10	69	20	10	0	10	0	0	10	30	256	88	29	10
5-6JUNE93	0	0	39	0	20	0	0	0	0	0	20	0	20	20	0	20	0	20	0	39	0	0	0	0	0	0	315	177	0	0
7-8JUNE93	0	0	0	0	0	20	0	20	0	20	0	0	0	20	39	0	20	0	0	20	0	0	0	0	0	0	79	79	0	0
9-10JUNE93	0	0	0	0	20	0	0	0	0	0	0	0	0	0	20	0	0	0	0	20	0	0	0	0	20	20	79	59	0	0
11-12JUNE93	0	0	0	0	0	0	20	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	59	0	0	0
13-14JUNE93	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0
SUM	173	57	197	273	98	128	102	295	61	152	610	301	284	221	124	119	169	314	82	162	105	89	238	98	221	152	1599	1034	77	64

Date / Site	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2	Mean	Stdev
20-21MAY93	20	10	10	10	20	10	20	39	59	10	10	0	49	20	10	10	39	20	0	10	10	10	59	49	0	20	0	10	19	16
22-23MAY93	0	0	0	0	10	0	0	0	20	20	0	0	39	29	0	0	10	20	0	0	10	10	79	59	0	10	10	0	13	19
24-25MAY93	0	10	0	0	10	10	20	10	0	29	0	10	59	39	10	0	0	39	29	0	20	0	79	138	10	0	10	10	20	25
26-27MAY93	0	22	0	0	6	6	11	0	0	17	0	6	17	51	11	6	22	22	11	11	6	11	84	152	0	6	6	17	21	25
28-29MAY93	34	17	6	0	6	0	34	22	56	56	6	34	56	118	34	28	22	39	11	34	39	22	146	325	17	11	28	28	42	48
30-31MAY93	22	11	6	22	0	39	34	34	84	213	0	51	62	95	45	34	39	67	11	6	28	11	247	415	6	17	0	0	55	80
1-2JUNE93	6	6	17	17	6	6	17	17	45	79	11	6	22	79	11	0	11	17	6	6	17	0	174	213	6	11	6	6	33	48
3-4JUNE93	0	10	20	20	10	10	49	0	59	128	29	10	0	10	0	0	59	69	0	39	10	0	226	246	20	20	20	20	49	65
5-6JUNE93	10	0	0	39	0	10	39	39	39	10	0	0	0	39	0	0	0	10	0	0	0	0	98	118	10	0	0	0	19	48
7-8JUNE93	0	20	0	20	0	0	0	0	20	20	0	0	20	20	0	0	20	0	20	0	0	0	79	118	0	20	0	0	11	23
9-10JUNE93	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	39	39	0	0	0	0	7	17
11-12JUNE93	0	0	0	0	0	0	0	0	0	0	0	0	0	39	0	0	59	0	0	0	0	0	0	0	0	0	0	0	4	13
13-14JUNE93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	1	5
SUM	92	106	59	128	68	91	224	161	382	582	56	117	344	539	121	78	301	303	88	106	140	64	1310	1872	69	115	80	91	294	431

APPENDIX IV

Soil Data of 88 Sites

Soil and site data

Factor / Site	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2
Soil pH	6.1	6.3	5.6	5.6	5.3	6.0	5.6	5.9	5.6	5.1	5.8	4.3	4.0	4.4	4.5	4.1	4.0	4.1	4.6	4.5	5.0	6.1
Soil organic matter (%)	80.8	80.8	86.1	86.1	90.3	90.3	86	86	84.6	84.6	33.4	33.4	33.2	33.2	74	74	66.3	66.3	46.5	46.5	74	74
Soil moisture (%)	57.1	57.1	60.2	60.2	70.2	70.2	65.3	65.3	62.1	62.1	36.4	36.4	29.9	29.9	55.1	55.1	43.5	43.5	30.1	30.1	55.5	55.5
Slope degree	0	3	8	5	0	0	12	15	0	3	2	2	0	0	2	2	2	2	0	0	2	2
Slope direction	0	150	190	130	0	0	130	160	0	310	210	200	0	0	240	240	150	135	0	0	220	140
Tree coverage (%)	86	64	70	54	67	76	70	42	5	16	84	53.5	34	31	82	66	73.5	59	40.5	52.5	72	76

Factor / Site	6L1	6L2	7R1	7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2
Soil pH	4.7	5.8	5.4	4.8	6.0	6.7	5.6	5.9	4.8	4.3	5.7	5.6	5.4	4.6	4.4	4.8	5.2	4.5	6.3	5.0	5.0	4.8
Soil organic matter (%)	21.9	21.9	79.3	79.3	69.7	69.7	75.3	75.3	68.9	68.9	28.3	28.3	82.5	82.5	56.4	56.4	74.2	74.2	4.5	4.5	68.4	68.4
Soil moisture (%)	24.4	24.4	50.6	50.6	53.7	53.7	71	71	54.3	54.3	39	39	80	80	53	53	49.3	49.3	13.8	13.8	50.3	50.3
Slope degree	2	2	3	10	2	2	0	0	2	12	0	5	0	2	15	15	10	15	20	22	5	2
Slope direction	240	90	150	70	210	230	0	0	60	120	0	70	0	240	310	350	290	180	310	130	180	180
Tree coverage (%)	66	82.5	60	51.5	85.5	27.5	65	47	58	9.5	72	53.5	51.5	76.5	26	33	56	61.5	40	19	79.5	68.5

Factor / Site	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1	15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2
Soil pH	5.8	5.2	5.3	5.3	4.8	4.3	4.2	4.5	5.1	5.1	5.0	4.3	4.7	3.7	6.2	6.5	4.4	3.9	5.7	5.8	3.7	3.7
Soil organic matter (%)	79.3	79.3	8.8	8.8	48.8	48.8	74.9	74.9	38.4	38.4	17	17	57.2	57.2	25.7	25.7	71.3	71.3	17.5	17.5	67.3	67.3
Soil moisture (%)	63.2	63.2	14.5	14.5	76.8	76.8	57.4	57.4	36.8	36.8	20.2	20.2	73	73	21	21	57.9	57.9	47.8	47.8	59.5	59.5
Slope degree	8	10	2	5	0	0	3	2	23	2	3	5	3	2	2	2	0	0	0	2	0	2
Slope direction	230	150	190	180	0	0	340	10	120	170	170	180	170	50	210	210	0	0	0	40	0	180
Tree coverage (%)	84	47.5	65.5	8	26.5	65.5	50.5	80.5	0	19	13	51.5	59.5	16	70.5	50	51	55	48	61.5	44.5	34

Factor / Site	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
Soil pH	5.7	3.8	4.1	4.5	4.7	4.9	4.6	4.5	5.0	5.3	4.9	4.4	5.6	5.9	3.9	4.3	6.1	6.3	4.1	4.4	4.8	4.4
Soil organic matter (%)	72.4	72.4	75.2	75.2	50	50	38	38	80.9	80.9	15.5	15.5	75.9	75.9	54.3	54.3	8.6	8.6	34.9	34.9	60.5	60.5
Soil moisture (%)	75.2	75.2	41.7	41.7	73.2	73.2	32.2	32.2	79.8	79.8	15.9	15.9	85.5	85.5	45.2	45.2	21.9	21.9	22.7	22.7	41.9	41.9
Slope degree	0	0	8	30	2	3	2	15	0	0	20	20	2	2	10	25	2	2	20	25	15	15
Slope direction	0	0	15	110	220	250	165	320	0	0	210	190	150	150	320	340	250	240	130	160	180	180
Tree coverage (%)	31	31	44.5	63.5	39	3.5	52.5	39.5	19.5	61	45.5	47.5	31	17	28	17	17.5	14.5	79.5	60.5	75.5	86

APPENDIX V

Chytrid Infestation Data

[Chytrid infestation (% grains infested after 10 days of incubation) of jack pine pollen added as bait to flooded soil samples collected in 88 boreal Manitoba sites, 7 times in 1992 and 1993]

Chytrid infestation data (1)

Species / Site (June 26, 1992)	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1
Spizellomyces papillatum	0	0	0	0	0	0	0	0	0	0	0	3	14	0	0	9	8	7	0	0	0	0	0	0	0
Rhizophydium sphaerotheca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
Chytriomyces annulatus	0	0	0	0	0	4	0	0	0	0	0	53	2	2	0	0	1	1	0	1	0	1	0	0	0
Spizellomyces reinboldtae	0	0	0	0	0	0	0	0	0	0	1	8	0	2	0	0	3	0	0	0	0	0	0	0	0
Chytriomyces poculatus	0	0	16	0	0	0	4	0	0	5	0	0	0	3	0	0	29	6	0	0	1	1	0	0	0
Rhizophydium pollinis-pini	0	0	0	0	7	0	4	0	13	4	3	0	12	24	0	0	2	5	0	0	11	0	0	0	0
Rhizophydium sp.-Phlyctochytrium aurilae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phlyctochytrium planicorne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other spp.	3	2	0	2	0	2	0	0	0	0	0	0	0	0	4	0	0	0	20	21	0	4	3	1	0
Sum	3	2	16	2	7	6	8	0	13	9	4	64	28	31	4	9	43	19	20	22	12	6	3	1	19

Species / Site (July 21, 1992)	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1
Spizellomyces papillatum	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	68	5	0	0	0	0	0	0	0
Rhizophydium sphaerotheca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	18	0	0	0	0	0
Chytriomyces annulatus	0	0	0	0	0	0	0	0	0	0	0	53	0	0	0	0	0	0	1	0	0	0	0	0	0
Spizellomyces reinboldtae	0	0	0	0	0	0	0	0	13	2	0	7	1	0	0	0	1	1	0	0	0	0	0	0	0
Chytriomyces poculatus	0	0	4	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Rhizophydium pollinis-pini	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	12	38	0	0	0	0	0
Rhizophydium sp.-Phlyctochytrium aurilae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phlyctochytrium planicorne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other spp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0
Sum	0	0	4	1	0	0	0	0	15	2	0	77	1	9	0	0	70	6	16	78	0	0	0	0	0

Species / Site (Nov. 3, 1992)	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1
Spizellomyces papillatum	0	0	0	0	0	0	0	0	0	0	1	0	0	21	0	6	60	0	2	0	0	0	0	2	0
Rhizophydium sphaerotheca	0	0	0	0	0	0	6	0	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Chytriomyces annulatus	0	0	0	0	0	0	0	0	0	0	56	0	0	0	0	0	7	0	0	0	0	0	0	0	0
Spizellomyces reinboldtae	0	0	0	0	0	0	0	0	0	0	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chytriomyces poculatus	0	0	23	0	5	0	0	11	0	0	3	24	18	47	62	66	6	42	61	70	5	64	60	76	0
Rhizophydium pollinis-pini	0	0	0	0	11	0	0	0	0	0	0	0	29	0	0	0	0	0	6	0	0	0	0	0	0
Rhizophydium sp.-Phlyctochytrium aurilae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phlyctochytrium planicorne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other spp.	2	7	0	10	0	2	3	7	0	0	0	0	0	3	2	0	1	0	2	0	0	0	12	0	
Sum	2	7	23	10	16	2	9	18	6	6	67	25	47	68	65	74	73	43	69	72	5	64	60	90	6

Species / Site (May 21, 1993)	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1
Spizellomyces papillatum	0	0	0	0	0	0	0	0	0	0	0	4	54	0	0	42	14	2	2	30	0	0	0	0	0
Rhizophydium sphaerotheca	0	0	0	16	40	12	0	50	32	16	0	0	0	6	0	8	8	24	6	0	50	18	20	34	0
Chytriomyces annulatus	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	2	0	0	0	0	0
Spizellomyces reinboldtae	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chytriomyces poculatus	0	0	0	26	16	0	0	0	0	0	0	0	0	88	0	26	78	2	2	0	0	2	62	0	0
Rhizophydium pollinis-pini	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0
Rhizophydium sp.-Phlyctochytrium aurilae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phlyctochytrium planicorne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other spp.	16	36	0	0	0	0	2	0	2	0	0	4	0	0	0	0	0	0	0	8	0	0	0	0	0
Sum	16	36	0	42	56	12	2	50	36	16	0	14	62	94	0	76	100	28	10	40	50	20	82	34	0

Chytrid infestation data (2)

Species / Site (June 17, 1993)	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1
Spizellomyces papillatum	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	3	0	0	13	0	0	0	0	0
Rhizophydium sphaerotheca	0	0	20	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chytriomyces annulatus	0	0	0	0	0	0	0	0	0	0	0	10	31	4	0	3	0	0	6	0	0	0	1	0	0
Spizellomyces reinboldtae	0	0	0	0	0	0	0	0	37	25	0	2	0	0	0	0	0	0	0	5	0	0	0	0	0
Chytriomyces poculatus	0	0	0	4	0	0	0	0	0	0	0	0	0	10	0	0	26	0	0	17	0	0	2	0	0
Rhizophydium pollinis-pini	0	0	0	0	0	0	0	0	0	0	0	0	4	4	0	0	0	1	0	0	0	0	0	0	0
Rhizophydium sp.-Phlyctochytrium aurilae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phlyctochytrium planicorne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other spp.	0	5	0	0	0	12	1	1	0	0	0	0	0	0	0	0	0	0	6	2	0	0	0	1	0
Sum	0	5	20	4	6	12	1	1	37	25	0	12	43	18	0	3	29	1	12	37	0	0	3	1	0

Species / Site (Aug. 21, 1993)	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1
Spizellomyces papillatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhizophydium sphaerotheca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chytriomyces annulatus	0	0	0	0	0	0	0	0	0	0	0	84	7	0	0	1	0	0	0	0	0	0	0	0	0
Spizellomyces reinboldtae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chytriomyces poculatus	0	0	1	0	0	0	0	0	0	0	0	2	0	0	66	3	39	1	4	0	10	0	4	0	0
Rhizophydium pollinis-pini	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhizophydium sp.-Phlyctochytrium aurilae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phlyctochytrium planicorne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other spp.	0	2	0	5	17	0	0	0	41	74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sum	0	2	1	5	17	0	0	0	41	74	0	86	8	0	66	4	39	4	4	15	10	0	4	0	1

Species / Site (Oct. 9, 1993)	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1
Spizellomyces papillatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	1	1	0	0	0	0	0	0
Rhizophydium sphaerotheca	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0
Chytriomyces annulatus	0	0	0	0	0	0	0	0	0	0	0	43	97	0	0	36	1	4	22	12	0	0	0	0	0
Spizellomyces reinboldtae	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	1	2	5	0	0	0	0	0	0
Chytriomyces poculatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhizophydium pollinis-pini	0	0	0	0	0	0	0	0	0	0	0	0	0	8	3	0	0	0	0	0	0	0	0	0	0
Rhizophydium sp.-Phlyctochytrium aurilae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phlyctochytrium planicorne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	43	0	0	1	0	0
Sum	0	0	1	0	0	0	0	0	5	0	0	43	97	8	3	39	3	7	35	55	0	0	1	0	0

7 times mean (1992 - 1993)	1R1	1R2	1L1	1L2	2R1	2R2	2L1	2L2	3R1	3R2	3L1	3L2	4R1	4R2	4L1	4L2	5R1	5R2	5L1	5L2	6R1	6R2	6L1	6L2	7R1
Spizellomyces papillatum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	3.4	10.9	3.0	0.0	8.6	22.0	2.1	0.7	6.1	0.0	0.0	0.0	0.3	0.0
Rhizophydium sphaerotheca	0.0	0.0	2.9	2.3	6.6	1.7	0.9	7.1	5.6	3.1	0.0	0.0	0.0	0.9	0.0	1.1	1.1	3.4	2.3	2.6	7.1	2.6	2.9	4.9	3.6
Chytriomyces annulatus	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	8.0	35.6	19.6	0.9	0.0	5.7	1.3	0.7	4.1	2.1	0.0	0.1	0.1	0.0	0.0
Spizellomyces reinboldtae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	3.9	1.1	2.6	0.1	0.3	0.0	0.0	0.7	0.9	0.7	1.0	0.0	0.0	0.0	0.0	0.0
Chytriomyces poculatus	0.0	0.0	6.4	4.3	3.0	0.0	0.6	1.6	0.3	0.7	0.4	3.7	2.6	21.1	18.6	13.6	25.6	7.3	9.6	12.4	2.3	9.6	18.3	10.9	0.0
Rhizophydium pollinis-pini	0.0	0.0	0.0	0.0	2.6	0.0	0.6	0.0	1.9	0.6	0.4	0.0	7.7	6.4	0.4	0.0	0.3	0.9	2.6	5.4	1.6	0.0	0.0	0.0	0.0
Rhizophydium sp.-Phlyctochytrium aurilae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phlyctochytrium planicorne	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other spp.	3.0	7.4	0.0	2.6	2.4	2.3	0.9	1.1	6.1	10.6	0.0	0.6	0.0	0.0	1.0	0.3	0.0	0.1	3.7	15.9	0.0	0.6	0.6	2.0	0.1
Sum	3.0	7.4	9.3	9.1	14.6	4.6	2.9	9.9	21.9	18.9	10.1	45.9	40.9	32.6	20.0	29.3	51.0	15.4	23.7	45.6	11.0	12.9	21.9	18.0	3.7

Chytrid infestation data (3)

7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1
0	0	0	0	0	0	13	0	0	0	0	18	4	0	1	0	10	3	0	0	0	0	0	0	0	29	0	12	1	3	38	0
0	0	1	0	13	46	0	0	0	0	0	0	0	0	0	2	55	15	13	23	42	2	0	0	58	0	0	0	0	0	0	0
0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	8	0
0	0	4	0	0	0	0	0	0	0	0	17	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	7	4	0	0	0	0	0	0	0
0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0
0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	12	6	0	0	0	0	0	0	0	0	0	0	49	2	0	0	0
0	0	5	0	19	46	17	0	1	28	0	66	4	0	1	27	71	18	13	23	42	16	0	7	62	36	0	72	3	3	46	0

7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1
5	0	0	0	0	0	28	0	0	0	3	7	2	0	2	14	14	2	55	0	0	0	0	0	0	40	3	1	0	0	12	0
0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	5	0	5	0	0	0	0	0	0	0	0	0	0	0	1	0	62
0	0	0	0	0	0	14	0	0	0	0	0	0	0	33	0	56	0	0	0	0	0	0	0	0	21	3	16	0	0	28	0
0	0	0	0	0	1	0	0	0	0	0	8	0	0	0	26	15	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	47	56	0	0	0	0	0	0	5
0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	26	0	0	0	0	23	2	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0	0
0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	23	1?	42	0	0	0	3	28	2	12	35	45	85	7	81	0	0	24	0	70	58	81	7	68	3	1	40	67

7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1
19	0	0	0	0	0	28	0	0	0	0	34	22	1	31	8	3	0	0	0	0	0	1	0	0	62	33	41	2	2	24	0
28	30	0	9	7	13	0	79	0	0	6	0	4	28	0	0	0	7	21	58	4	0	0	72	48	0	0	0	0	0	0	0
0	0	0	0	0	0	45	0	0	0	0	5	0	0	1	0	55	0	0	0	0	0	0	0	0	18	9	15	0	0	0	0
0	0	10	0	0	0	0	0	0	0	0	1	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	32	0	0
0	0	0	0	0	21	0	0	0	56	40	8	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	2	3	0	53	0
0	0	0	0	0	0	0	0	0	10	9	0	0	0	0	0	0	0	0	0	0	0	0	1	20	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	48	2	0	1	0	0	0	0	0	0	0
0	0	0	0	4	0	0	0	0	1	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	30	10	9	11	34	73	79	1	67	82	48	26	29	32	15	58	7	21	58	4	48	3	75	71	80	42	58	5	34	77	0

7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1
24	0	0	0	0	0	22	0	0	0	4	4	14	0	10	0	30	0	0	0	4	6	2	10	0	18	10	10	6	40	48	0
0	4	0	0	0	16	0	0	0	0	12	8	0	8	6	0	6	50	44	12	0	2	0	74	36	0	24	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
20	38	0	0	0	2	60	24	0	0	0	52	0	4	0	0	0	32	0	76	12	0	0	4	2	8	52	0	0	0	0	14
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	14
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0
0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
44	42	0	2	8	18	82	24	0	0	16	64	14	12	16	0	36	82	44	88	16	26	4	88	38	48	86	14	6	44	48	28

Chytrid infestation data (4)

7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1
1	0	0	0	0	0	10	0	0	0	0	2	3	0	35	0	0	0	0	0	12	0	0	0	0	14	0	0	0	0	10	0
0	0	0	0	42	3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	8	0	0	28	0	0	23	0	0	0	0
2	0	0	0	0	0	45	0	0	0	0	45	0	0	3	5	58	0	0	0	0	0	0	0	0	38	0	0	0	0	66	0
0	0	5	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0
52	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	45	0	0	0	0	0	0	3	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	1	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41	0	0	18	0	0	38	1	1	0	0
55	0	5	1	43	25	55	0	0	0	0	50	3	0	38	5	58	0	0	2	13	57	0	86	48	52	0	83	1	1	79	0

7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	0	0	0	0	53	0	0	0	0	1	0	4	13	0	0	0	0	0	16	0	0	0	0	83	23	0	9	0	26	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	11	0	0	2	3	0	0	0	13	0	0	0	38	0	0	0	0	0	0	67	0	0	17	1	0	0	0	1	0	27	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	0	0	0	0	0	0	0	25
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	2	0	33	0	0	0	0	0	2	0	0	0	2	1	1	0	0	0	76	68	0	42	0	0	0	77	1	2	0
76	12	0	2	3	36	53	0	0	13	0	3	0	42	13	2	1	1	0	0	83	76	68	51	43	83	23	0	87	2	56	28

7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1
2	0	0	0	0	0	5	0	0	0	1	9	2	0	2	0	1	3	1	0	1	0	0	0	0	7	2	2	1	1	3	0
0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	78	0	0	0	98	91	0	0	1	0	0	0	1	0	0	0	0	76	51	90	95	58	0	33	96	0
3	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	22	0	0	0	0	0	0	9
0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	1	0	5	4	83	0	0	0	99	100	4	0	3	6	3	8	3	0	1	98	0	77	77	97	97	60	1	34	99	9

7R2	7L1	7L2	8R1	8R2	8L1	8L2	9R1	9R2	9L1	9L2	10R1	10R2	10L1	10L2	11R1	11R2	11L1	11L2	12R1	12R2	12L1	12L2	13R1	13R2	13L1	13L2	14R1	14R2	14L1	14L2	15R1
7.3	0.0	0.0	0.0	0.0	0.0	15.1	0.0	0.0	0.0	1.1	10.6	6.7	0.1	11.6	3.1	8.3	1.1	8.0	0.0	2.4	0.9	0.4	1.4	0.0	24.3	6.9	9.4	1.4	6.7	19.4	0.0
4.9	4.9	0.1	1.3	9.0	13.1	0.0	11.3	0.0	0.0	2.6	1.1	0.7	5.1	0.9	1.0	8.7	11.7	11.3	13.6	6.6	1.7	0.0	20.9	24.3	0.0	3.4	3.3	0.0	0.1	0.0	8.9
1.1	0.1	0.0	0.0	0.0	0.0	34.1	0.0	0.0	0.0	14.0	20.4	0.0	0.6	7.3	0.7	24.1	0.0	0.1	0.0	2.3	0.0	0.0	10.9	7.3	36.7	18.6	13.6	1.3	4.7	32.0	0.0
0.4	0.0	2.9	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	4.1	0.1	0.0	0.0	6.6	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.0	5.1	0.0	0.0
20.0	7.0	0.0	0.0	0.3	7.4	8.6	3.4	0.0	9.9	5.7	12.9	0.0	7.7	0.0	0.0	0.0	4.6	0.0	10.9	11.3	0.0	0.0	15.9	8.9	1.1	7.4	0.3	0.6	0.0	11.4	3.1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.4	1.3	1.9	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.1	0.0	0.0	15.9	6.9	3.1	0.1	0.0	0.0	0.0	0.4	6.9
0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.1	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.7	0.4	4.7	0.0	0.0	0.3	0.0	1.0	0.3	0.0	0.0	0.0	2.9	1.3	0.1	0.0	0.0	0.0	30.7	10.0	0.0	9.1	2.9	0.0	19.3	11.9	0.3	0.3	0.0
33.7	12.0	3.0	2.0	16.0	25.4	57.9	14.7	0.3	15.4	28.6	51.3	7.6	13.6	19.7	14.3	44.6	17.6	23.1	24.4	22.7	49.3	10.7	64.9	56.7	68.1	36.4	50.7	15.1	17.0	63.6	18.9

Chytrid infestation data (5)

15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
60	0	0	8	16	0	0	1	1	0	1	44	1	1	0	0	0	28	3	31	0	0	0	2	15	0	0	1	1	0	53
0	76	61	0	15	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	75	0
1	0	0	0	20	0	0	0	0	0	0	0	0	4	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	60	0	0	38	0	0	0	0	83	0	0	0	0	5	0	0	82	0	0
0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	53	0	0	0	0	0	1	0	0	0	0	0	0	3	33
0	0	0	0	0	0	0	15	0	86	21	0	0	54	0	0	0	1	0	1	0	59	13	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	76	61	8	53	0	1	16	1	86	22	44	61	59	8	38	53	31	7	32	83	59	15	2	15	5	0	1	83	78	88

15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
0	18	0	32	2	2	0	40	0	1	7	0	27	0	3	9	0	8	0	9	0	0	0	4	8	0	0	61	5	0	19
0	7	32	0	0	10	0	0	0	0	0	12	0	0	0	0	20	0	45	0	0	0	0	0	0	0	0	0	0	7	0
0	0	0	0	7	0	0	15	1	18	60	0	21	0	46	0	0	6	0	0	0	0	0	0	2	0	0	7	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	22	0	5	0	0	78	0	0	0	3	10	0	0	43	0	0
0	0	0	0	0	0	0	2	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	4	0	0	2
0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	6	0	0	0	0
0	25	32	32	9	14	0	57	1	40	67	12	49	0	60	31	20	19	48	10	78	18	1	4	13	10	6	72	46	25	21

15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
88	0	0	37	26	0	0	81	47	1	25	73	21	12	3	89	0	67	0	15	0	0	0	2	85	0	0	2	33	0	67
0	38	62	0	0	32	0	0	0	0	16	0	0	0	82	0	12	0	0	2	0	0	9	0	0	0	0	0	0	0	0
0	0	0	0	10	0	0	0	0	0	0	2	16	0	0	16	0	1	0	26	0	0	0	78	3	0	0	86	42	0	0
0	0	0	26	0	0	0	0	0	1	0	0	9	3	0	0	0	0	0	0	25	0	0	0	0	50	5	0	0	0	0
0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	5	12	0	0	3	5	0	0	0	0	0	0	0	12
0	0	0	3	0	0	0	0	0	0	8	0	0	0	0	0	0	0	7	0	0	22	1	0	0	0	0	0	0	0	7
0	0	0	0	0	1	0	0	0	1	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	38	62	67	36	33	0	81	47	4	52	75	84	15	85	85	12	73	19	43	25	25	15	80	89	50	5	88	75	0	86

15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
0	0	0	36	28	0	0	12	0	0	2	64	42	16	0	48	0	56	0	32	0	0	0	60	22	0	0	68	74	0	16
0	20	40	0	0	8	64	0	52	72	0	0	0	0	12	0	6	0	0	4	0	0	0	0	0	0	0	8	2	0	12
0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0
0	0	0	28	28	42	0	2	2	0	0	4	0	0	44	0	0	14	42	0	0	58	6	0	4	0	0	0	0	0	34
16	0	0	0	0	4	0	42	0	0	32	0	0	0	0	0	0	0	18	0	0	0	0	4	0	0	8	0	0	0	0
0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
16	20	40	64	60	54	64	56	56	72	34	68	42	16	58	48	6	70	60	36	28	58	6	64	26	2	8	76	76	0	62

Chytrid infestation data (6)

15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
0	0	0	2	7	0	0	7	0	0	0	11	2	0	4	2	0	13	12	4	0	0	0	2	0	0	0	48	0	0	3
0	0	16	0	0	3	0	0	0	5	0	0	0	0	0	0	62	55	42	0	0	24	24	0	0	0	0	0	0	0	0
0	0	1	53	36	0	0	28	0	0	16	35	63	0	66	31	2	4	0	56	0	0	0	74	73	0	0	31	80	0	31
0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	15	0	0	0	0	95	0	0	0	0	36	5	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	0	2	0	0	0	9	0	15	0	0	12
0	0	0	14	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	0	1	0	0	21
0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	84	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	17	69	46	4	0	36	84	7	16	46	85	1	70	48	64	72	73	60	95	26	24	79	75	45	5	95	80	0	67

15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
0	0	62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39	0	0	0	0	0	0	0	0	0
34	0	1	47	4	0	0	31	0	0	54	69	94	65	0	0	98	0	2	73	57	0	0	62	32	0	0	55	93	0	11
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	1	2	0	0	1	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	10	8	0	0	4	69	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41	35	0	0	0	0	0	0	0	0	0	0	0	0
1	1	0	0	0	51	0	0	0	94	0	0	0	0	0	29	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
35	1	63	58	14	51	0	36	69	94	56	69	94	65	13	29	98	41	37	73	58	0	39	63	32	3	0	55	93	14	12

15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
0	0	0	0	1	0	0	1	0	0	1	2	0	0	0	5	0	2	3	0	0	0	0	3	3	0	0	10	1	0	0
0	35	28	0	0	0	0	0	0	0	0	0	0	63	0	18	90	0	73	0	0	18	17	0	0	0	0	0	0	0	0
61	0	0	93	90	0	0	86	0	70	89	93	97	18	0	2	0	95	0	4	0	0	0	93	78	0	0	82	88	0	12
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	73	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0	12	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	26	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	35	28	93	91	0	0	86	0	96	90	95	98	93	0	25	90	97	87	4	73	18	17	96	81	0	0	92	90	0	12

15R2	15L1	15L2	16R1	16R2	16L1	16L2	17R1	17R2	17L1	17L2	18R1	18R2	18L1	18L2	19R1	19R2	19L1	19L2	20R1	20R2	20L1	20L2	21R1	21R2	21L1	21L2	22R1	22R2	22L1	22L2
21.1	2.6	0.0	16.4	11.4	0.3	0.0	20.3	6.9	0.3	5.1	27.7	13.3	4.1	1.4	19.0	0.0	24.9	2.6	13.0	0.0	0.0	0.0	10.4	19.0	0.0	0.0	27.1	16.3	0.0	22.7
0.0	25.1	43.0	0.0	2.1	7.6	9.1	0.0	7.4	11.0	2.3	1.7	0.0	9.0	14.6	2.6	27.1	7.9	22.9	0.9	0.0	6.0	12.7	0.0	0.0	0.0	0.0	1.1	0.3	11.7	1.7
13.7	0.0	0.3	27.6	23.9	0.0	0.0	22.9	0.4	12.6	31.3	28.4	41.6	12.4	16.3	7.0	14.3	15.4	0.9	22.7	8.1	0.0	0.0	43.9	26.9	0.0	0.0	37.3	43.3	0.0	7.7
0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	12.9	0.4	0.0	10.7	0.0	0.7	0.0	0.0	54.7	0.0	0.0	0.0	0.4	14.4	1.4	0.0	18.0	0.0	0.0
0.0	0.0	0.0	4.3	4.7	6.0	0.0	0.7	0.3	0.0	0.4	0.6	0.0	0.0	9.7	0.0	7.6	2.7	10.4	0.0	0.0	9.0	1.7	0.1	0.6	1.3	0.0	2.1	0.0	3.0	13.0
2.3	0.0	0.0	3.9	1.4	0.6	0.0	9.0	9.9	12.3	9.0	0.0	0.0	9.4	0.0	0.0	0.0	0.1	5.1	0.1	0.0	14.1	2.0	1.0	0.3	0.0	1.1	0.7	0.0	2.0	4.6
0.0	0.0	0.0	0.0	0.6	0.6	0.0	0.0	0.0	0.3	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	5.1	0.0	0.0	0.0	0.3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
0.3	0.3	0.0	0.0	0.0	7.3	0.1	0.0	12.0	20.3	0.0	0.0	3.6	0.1	0.0	4.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.7	0.9	0.0	0.0	0.0	0.0
37.4	28.0	43.3	55.9	44.1	22.3	9.3	52.9	36.9	57.0	48.1	58.4	73.3	35.6	42.0	43.4	49.0	57.6	47.3	36.9	62.9	29.1	16.7	55.4	47.3	16.4	3.4	68.4	77.9	16.7	49.7

APPENDIX VI

Chytrid Species Descriptions

[Chytrid species occurred on jack pine pollen added as bait to flooded soil samples collected in 88 boreal Manitoba sites, 7 times in 1992 and 1993]

Chytrid species descriptions

Chytriomyces annulatus Dogma (Nova Hedwigia 18: 349, Figs. 1-18, 1969)

On pine pollen mature spherical sporangia are 10-16 μm. Pyriform sporangia are 13-20 μm high and 9-14 μm wide. Ring-like undulations usually occur on the sporangium wall near the origin of the rhizoidal system. Occasionlly rings appear well up on the wall.

This species was collected by Dogma (1969) with leaf and soil samples from the Douglas Lake region in Michigan and other sites (Gate's Bog [type locality], Cheboygan Co., Grapevine Point, Cross Village, Big Bay, Round Lake, Sugar Island, Michigan; Wisconsin; edge of Silver Lake, North Carolina; top of Acadia National Park, Maine; Peterburg, Virginia; Forest Lake State Park, New Hampshire; top of Burke Mt., Vermont). This species was collected by Booth and Barrett (1971) from Devon Island, Canadian Eastern Arctic (ice wedge polygon sites, a raised beach slope collection) who reported that arctic samples were collected from acidic sites. Booth and Barrett (1976) collected this species from soils of Truelove Lowland, Devon Island . Also Booth (1979) collected this chytrid from dune depressions with litter covered sands in beach and coastal habitats in Brazil . Booth (1981) collected this species from arctic marine site near Hudson Bay .

Chytriomyces poculatus Willoughby and Townley (Trans. Brit. Mycol. Soc. 44: 183, Fig. 3, 1961)

Thallus monocentric, eucarpic, consisting of an epibiotic sporangium and a single delicate rhizoid. Sporangia mostly ellipsoid 15-24 μm long by 8-16 μm wide, subglobose or pyriform sporangia also occur rarely. The sporangium surface is ornamented with up to 10, thin, overlapping cupules of wall material.

This species is chatacterized by a type of sporangium ornamentation which appears to be unique in the chytrids, consisting of a series of thin overlapping cupules of wall material.

This species was originally isolated from soils of the English Lake District (Willoughby and Townley 1961). Also it was obtained from soil samples collected at Shap and Naddle Forest (east of Haweswater) and at Haile (N.W. of Wastwater). All three samples were peaty and the pH of the liquid in the baiting dishes (5-5.6) was somewhat lower than that usually recorded (Willoughby and Townley 1961). Willoughby (1962) collected this species from English Lake District, England - *C. poculatus* and *Septosperma rhizophidii* were obtained only at low pH values (5.1-5.7). Willoughby (1965) isolated this species from soils in Australia . Dogma (1969) isolated this species from leaves and Sphagnum samples from Michigan (on pine pollen; Sphagnum samples, Sugar Island; Chippewa Co.; Wycamp Woods, Emmet Co.; Mud Lake, Cheboygan Co.; Bryant's Bog; soil and leaf litter samples, Emmet Co.). Booth (1969) collected this species from coastal and Interior halomorphic soils from British Columbia . Also coolected by Booth (1971a,b) from soils of southwestern British Columbia and the San Juan Islands, and Hibben and Moresby Islands, Queen Charlotte Islands (coastal western hemlock sites, flushes, blanket bog sites, a tidal edge, a marine high beach site, and an alpine meadow location). Booth (1971d) isolated this species from coastal western hemlock sites, beach cliff. From soils of Truelove Lowland, Devon Island (Booth and Barrett 1976). Bandoni and Barr (1976) reported that *C. poculatus* developed on sterile pine pollen. They showed that a washed segment of decaying *Alnus rubra* stem was the source of *C. poculatus*; this twig was collected in a relatively moist forested area in Vancouver. Booth (1979) reported this species from dune depressions with litter covered sands, on dune crests and in forest sands in Brazil .

1962) isolated this species from Esthwaite water, England and English Lake District. Miller (1965b) reported this species from Mountain Lake in Virginia. Sparrow et al. (1965) reported this species on *Closterium turgidum* var. *giganteum* used as bait in water from Jewett Lake, Rifle River Area, Ogemaw Co., Michigan. Karling (1966, 1967b) reported this species on *Spirogyra* sp., Poondi, Madras State in India and on dead bits of sclerenchyma in soil sample, New Zealand. Milanez (1967) reported this species from a water sample taken from the outlet of Gull Lake, Kalamazoo Co., Michigan, which yielded a colony of *Achlya oligacantha* de Bary heavily parasitized by *P. planicorne*, with both zoosporangial and resting spore thalli and on pine pollen used as bait . Dogma (1969) reported this species on pine pollen in water cultures of bottom organic debris from Smith's Bog, Cheboygan Co., Michigan. Kazuko (1972) this species Parasitizing on *Spirogyra* sp., Nagatoro in Japan. (Johnson 1973, 1977) recovered initially on autoclaved pine pollen (*Pinus taeda* L.) baited in water from a bog (*Sphagnum* spp.) bordering Gravtjern and Bakketjern, Norway and Iceland. Wang and Chien (1992) reported this species from northern Taiwan. Chen and Chien (1995) isolated this species from Tungshih wooded land, lake, Taiwan.

Phyctochytrium reinboldtae Persiel (Arch. f. Mikrobiol. 32: 414, Fig. 1, 1959)

Sporangia mostly spherical 19-27 μm in diameter including several extended discharge tubes.

Originally observed by Reinboldt (1951) from ahalomorphic soils, *P. reinboldtae* has since been observed by several researchers in halomorphic soils. Gaertner (1954) studied several aspects of this fungus, including the influence of axenic culturing, the resting stage, and the effect of salt concentration on growth. Sparrow et al. (1965) found this species on pine pollen bait, soil, Grapevine Point,

Phlyctochytrium papillatum Sparrow (Mycologia 44: 764, Fig. 1, 1952)

Sporangium sessile, spherical, 18 - 26 μm in diameter. Resting spores sessile, brown in color, subspherical with a moderately thick wall beset with numerous stout, blunt papillae. Germination not observed.

Originally collected by Sparrow (1952), parasitic on pine pollen in soil from bank along Grapevine Point Trail, Biological Station, University of Michigan, Cheboygan Co., Michigan. Miller (1965b) found this species on sweet gum and corn pollen baits from Twin Springs and Atkins Pond, Virginia.

Phlyctochytrium planicorne Atkinson (Bot. Gaz. 48: 337, 1909)

This chytrid, described in 1909 by Atkinson on *Spirogyra varians*, has an apical crown of four plain teeth surrounding the exit pore of the sporangium. The sporangium at maturity was 8-12 μm in diameter by 12-16 μm in height, including four solid refractive teeth, which were about 3 μm in length. The rhizoids were variable in length.

Sparrow 1932 reported this species parasitizing in *Spirogyra* sp. and *Rhizoclonium heiroglyphicum*, Fish Hatchery Pond near Schoolhouse, R.I. Sparrow (1938) reported this species on *Rhizoclonium heiroglyphicum* at both Cold Spring Harbor, New York, and Cambridge, Massachusetts. Sparrow (1952) reported this species on oogonia of *Oedogonium* sp., Smith's Bog in Michigan. Also *P. planicorne* was collected from Mountain Lake growing on the vegetative hyphae of *Aphanomyces laevis* de Bary and the resting bodies of *Olpidiopsis aphanomycis* Cornu *sensu* Sparrow (1960), which was also parasitizing *A. laevis*. This species has previously been reported growing on the various algae and on the plant debris (Sparrow 1960) and on sweet gum and pine (*Pinus taeda* L.) pollen by Umphlett and Holland (1960). Willoughby (1961,

Douglas Lake in Michigan. Karling (1967b) found this on dead pollen of *Pinus sylvestris* in soil samples, New Zealand. Booth (1969) reported from Coastal and Interior halomorphic soils from British Columbia. A pure culture of *P. reinboldtae* Persiel isolated from soil near Ottawa, Canada, grew best at 20 and 25°C, slightly at 10°C, and not at all at 35°C (Barr 1970). It grew best in alkaline media and required no exogenous vitamins. This species was collected by Booth (1971a,b) from soils of southwestern British Columbia and the San Juan Islands, and Hibben and Moresby Islands, Queen Charlotte Islands (a coastal western hemlock site). Booth (1971d) found this on pollen, shrub steppes, dune, desert high beaches, volcanic ash slope, pond depression slope, evaporation flat, shrubless. Dogma (1975) found this species on pine pollen, soil, Mountain State agricultural college campus, La Trinidad, Philippine. Booth (1979) collected this from dune crest in beach and coastal habitats in Brazil. Karling (1981) found this on pine pollen in soil, Sri Lanka.

Rhizophydium pollinis-pini (Braun) Zopf (Abhandl. Naturforsch. Ges. Halle, 17: 82, Pl. 1, Figs. 16-20, 1887)

On pollen mature sporangia are 8-19 μ in diameter. Sporangia dehisce through a single apical papillum. Empty sporangia are urniform and occasionlly pseudointernal proliferation occurs. Rhizoids are once or many times branched.

Commonly on pine pollen, which has fallen in water, but has also been reported on pollen of other types, Cold Spring Harbor, Long Island (Sparrow 1932). Karling (1946) collected this species on fern spores and pollen grains, Brazil. Sparrow (1952) isolated this species on pine pollen, Smith's Bog in Michigan. Sparrow (1957) collected this from dead pollen of pine, Great Britain. Miller (1961) isolated this on sweet-gum and pine pollen baits, Buncombe Creek. Sparrow (1965) reported from pine pollen bait, soil, Kawaiiki Ditch Trail in Hawaii.

Karling (1967a) collected on dead pollen of *Pinus sylvestris* in soil samples, New Zealand. Karling (1968) reported this on pollen grains of *P. sylvestris* in soil sample, Cook Islands and American Samoa. Howard and Johnson (1969) collected this in soil and water samples from Iceland. Booth (1969) reported this from coastal and Interior halomorphic soils from British Columbia. This species was collected by Booth (1971b) from soils of Hibben and Moresby Islands, Queen Charlotte Islands (a beach site, and coastal western hemlock sites). Booth (1971d) observed this on pollen, beach plain site, evaporation flat, marine high beach, freshwater marsh. Booth and Barrett (1971) reported this from Devon Island, Canadian Eastern Arctic (ice wedge polygon sites, a raised beach ridge site, a *Carex* hummock subassociation, a snowbed-moss association and an *Arctagrostis latifolia* meadow). Kazuko (1972) obseved this on pine pollen, set in water and soils of brook, stream, paddy field, and forest, Tsugawa in Japan. Johnson (1973) collected this species from Iceland. Booth and Barrett (1976) collected from soils of Truelove Lowland, Devon Island .

Rhizophydium sphaerotheca Zopf (*sensu* Booth) (Can. J. Bot. 49: 962, Fig. 23, 1971)

Sporangia 13-26 μm in diameter with one to five papillae. One to five papillae pores occur in the sporangium wall distinctly double-contoured. Rhizoids fine and much branched, usually arising directly from sporangium base.

This species was collected by Booth (1971a,b) from soils of southwestern British Columbia and the San Juan Islands, and Hibben and Moresby Islands, Queen Charlotte Islands (disturbed sites, beach intertidal sites, coastal western hemlock sites, marine high beach sites, headland sites, flushes, a blanket bog site, tidal edge sites, a dune site, and a stream bank site). Booth (1971d) observed this species on pollen, coastal western hemlock site, beach plains, dunes, open

undifferentiated sand sites, beach cliff, tide affected stream site, desert lake water edge, shrub steppes, desert high beaches, pond depression slopes, evaporation flat, disturbed site, tidal edge, marine high beach. Also collected from Devon Island, Canadian Eastern Arctic (Booth and Barrett 1971). Kazuko (1972) observed this on pine pollen set in water, litter and soil, Hokkaido in Japan. Johnson (1973) collected this from Iceland. Dogma (1975) observed this species on pine pollen, in soils, Laguna, Albay, Sorsogon, Batangas, and Benguet, Philippine. Booth and Barrett (1976) collected from soils of Truelove Lowland, Devon Island. Also Booth (1979) collected this from toque soil in beach and coastal habitats in Brazil.

Rhizophydium sp.-***Phlyctochytrium aurilae*** Ajello complex (Mycologia 37: 109, Figs. 1-13, 1945)

Sporangia apophysate or non-apophysate, 20-28 μm in diameter with varying numbers and complexity of spines.

Ajello (1945) collected this species in decaying vegetable debris collected from a quiet stream at Lake Minnewaska, Ulster Co., New York and a bog on Bearfort Mountain, Passaic Co., New Jersey. Sparrow and M. Barr (1955) observed this on purified shrimp skeleton bait, debris from under ice, Bryant's bog, Michigan. Sparrow and Koch (1959) observed this on *Liquidamber* pollen bait, Bryant's Bog; Nichol's Bog; insect exuviae, Hardbottom Bog (Emmett Co.); snake skin bait, Bryant's Bog in Michigan. Sparrow (1965) observed this on chitin bait in debris of mosses and *Drosera anglica* from Wahiawa Bog in Hawaii. Also collected from various sites at Mountain Lake Biological Station, Virginia, and the University of Maine Forest, Orono, Maine (Miller 1968). This species was collected by Booth (1971b) from soils of Hibben and Moresby Islands, Queen Charlotte Islands (flushes, and a blanket bog site). Johnson (1973) collected this

from Iceland. Johnson (1977) found this species on baits in water, mud, and widely in bog areas in southern Norway and in Sweden.

Septosperma rhizophidii Whiffen (Mycology 34: 552, Figs. 28-52, 1942)

The sporangia are sherical and 8-18 μm in diameter. The clavate resting sporangia are 4-8 μm wide and 10-23 μm long. Paracitic on *Chytriomyces annulatus*, *Rhizophydium pollinis-pini* and *R. sphaerotheca*.

Parasitic on *Rhizophydium macrosporum* (Whiffen 1942). Parasitic on cyst of a microscopic animal, Bryant's Bog in Michigan (Sparrow 1952). On *Rhizophydium* spp. in Great Britain (Willoughby 1956). Parasitic on *Rhizidium richmondense*, *Rhizophydium elyensis* and *R. stipitatum*, England (Willoughby 1962). Parasitic on *Rhizophydium sphaerotheca* collected from Twin Springs and this relatively common fungus of sphagnous bogs was also collected on *Rhizophydium* sp. from Little Spruce Bog (Miller 1965b). Parasitic on *C. hyalinus* from soil sample, New Zealand (Karling 1967a). Coastal and Interior halomorphic soils from British Columbia (Booth 1969). This species was collected by Booth (1971b) on *Rhizophydium sphaerotheca*, *Chytriomyces hyalinus* and *C. poculatus* from soils of Hibben and Moresby Islands, Queen Charlotte Islands (flushes, a blanket bog site, a coastal western hemlock site, and a dune site). Parasitic on *Rhizophydium sphaerotheca* and *Rhizophydium* spp. from Gumma, Tokyo, Nara in Japan (Kazuko 1972).

APPENDIX VII

Temporal Distribution of Ectomycorrhizal Fungi in the Mistik Creek area, Manitoba

Temporal Distribution of Ectomycorrhizas

Ectomycorrhizal Sampling

Sampling for ectomycorrhizas was conducted at 2 sites in the study region. Soil samples consisted of cylindrical cores 10 cm (diameter) x 12.5 cm (depth) taken randomly at study site 5, a mature jack pine (*Pinus banksiana*) stand and site 6, a mature black spruce (*Picea mariana* (Mill.) BSP.) stand. Description of these specific study sites is seen in Chapter V of this dessertation.

On each of the collecting dates, 26 May, 18 June, 22 August, 10 October 1993 and 9 July, 31 July, 28 August 1994, 10 soil cores were gathered. Upon return to the laboratory, woody materials, mineral, and humus aggregates in the soil were removed before wet sieving through a 2-mm mesh for 5 minutes. Subsequent to cleaning, root samples were cut into 3-5 cm long segments and fixed in 50% ethanol. Visual assessment, at 12 to 25 times magnification, of the number of active ectomycorrhizas in a sample of 50 root tips was made from five cores for each site and date (Criteria used in identifying active ectomycorrhizal tips are described by Harvey et al. 1976). Total ectomycorrhizas for each the collecting dates is expressed as the mean percentage of active mycorrhizas from five cores at each site. Values for each core were scored as number of finds (active mycorrhizas) divided by number of starts (50 root fragments surveyed).

Temporal Pattern of Ectomycorrhizas

In both forest stands, ectomycorrhizas tended to be lower in the spring collections than in the summer and fall samples (see table this Appendix). Seasonal pattern of ectomycorrhizas in the jack pine stand (in needle litter) indicated a trend of summer (July through August) high numbers and spring and

fall lower numbers. Mycorrhizas on black spruce roots (in mixed leaf litter) were higher in summer and fall (October) than spring.

Like chytrid pollen infestations, formation of ectomycorrhizas were seasonal in the Mistik Creek study region. Ectomycorrhizal fungi are limited by low soil temperature (Bowen 1970; Marx et al. 1970; Theodorou and Bowen 1971) and excess moisture (Worley and Hackaylo 1959; Muttiah 1972). Generally, peak activity of ectomycorrhizal fungi is in the middle to end of each growing season in spruce and pine stands (Danielson and Pruden 1989; Wu et al. 1993). That ectomycorrhizal fungi depend on available carbon for enhanced growth, as demonstrated for *Suillus brevipes* in my study, is shown for soils and litters by Harvey et al. (1978, 1979) and Read (1984). Among the plant-derived organic materials that support ectomycorrhizal activity are pollen, litter, humus and decayed wood. In addition to carbon, ectomycorrhizal fungi require elements from organic and inorganic components of litter and soil (Linderberg 1986; Cairney and Ashford 1991; Pankow et al. 1991).

Table. Seasonal variations of active ectomycorrhizas in two forest stands in boreal Manitoba. Values are mean (± S.D. where n=5) percentage of active mycorrhizas from five samples at each site over the collecting dates.

Forest stand	May 26, '93	June 18, '93	Aug. 22,'93	Oct. 10, '93	July 9, '94	July 31, '94	Aug. 28,'94	Active Mycorrhizas (Mean %)
Jack Pine	55.2 ± 8.6	62.8 ± 8.9	68.4 ± 12.0	58.4 ± 6.7	78.0 ± 10.9	77.6 ± 8.8	78.4 ± 7.6	68.4 ± 9.9
Black Spruce	64.8 ± 13.1	71.8 ± 8.4	80.8 ± 8.6	78.8 ± 10.5	73.6 ± 8.1	71.2 ± 11.6	80.0 ± 11.9	74.4 ± 5.8

APPENDIX VIII

Suillus brevipes Hyphal Growth Experiment

Suillus brevipes Hyphal Growth Experiment

Jack Pine Pollen Collection

Male cones were collected, prior to anthesis, from the Mistik Creek study area in June 1993. Picked cones were placed on tin foil in the laboratory and dried for three days at room temperature. Shed pollen was subsequently gathered and separated from cone debris by sieving the grains through a 53 μm mesh. Once cleaned, pollen was stored in plastic bags and held at room temperature.

Isolation and Axenic Culture of Hyphae

Suillus brevipes (Pk.) Kuntze was collected from site 5. Cultures of this ectomycorrhizal fungus were obtained by plating excised stipe segments (~5mm cubed) on Melin Norkrans (MMN) medium as modified by Marx (1969). Bacterial contamination was eliminated by adding antibiotics (0.2 g penicillium G and 0.2 g streptomycin sulphate per liter to the medium). The isolate was subcultured and maintained in tubes at 4°C on MMN slants free of antibiotics.

Suillus brevipes Hyphal Growth Experiment

Standard fungal explants were prepared by removing 6 mm plugs from the margin of an actively growing colony developed at 20°C on a sugar agar medium containing 15 g agar, 10 g dextrose and antibiotics per liter. Prior to inoculation with fungal plugs, ten replicates of each pollen treatment: i) control, without pollen; ii) level 1, at 1.56 mg of pollen per plate; iii) level 2, at 6.25 mg (mean pollen deposition mass / unit area over the 88 collecting sites); iv) level 3, at 25 mg (4x mean pollen deposition); and v) level 4, at 100 mg (16x mean pollen deposition), were prepared by dusting freshly collected pine pollen onto the surface of water agar (15 g agar/liter and antibiotics) or the sugar agar, described

above, in plastic petri plates. Inoculated plates were incubated at 20°C during the day (16 hrs) and 15°C during the night (8 hrs). Plates were sealed with strips of paraffin film. Fungal growth was expressed as hyphal area (cm^2) measured after 15, 30 and 70 days.

Suillus brevipes Hyphal Growth Experiment

Growth of *Suillus brevipes* hyphae is generally better (increased hyphal area) in cultures containing dextrose carbon than in plates without sugar (Fig. A & B). Pollen additions increase the area covered by hyphae (Fig. A) and pollen stimulated growth is greater when dextrose is available to *S. brevipes* (Fig. B). Level 2 additions of pollen, representing mean pollen deposition (9 kg/ha) in Mistik Creek area, as well as level 3 (4x mean deposition) and 4 (16x mean deposition) additions, notably increase hyphal area after 30 and 70 days of growth with dextrose availability.

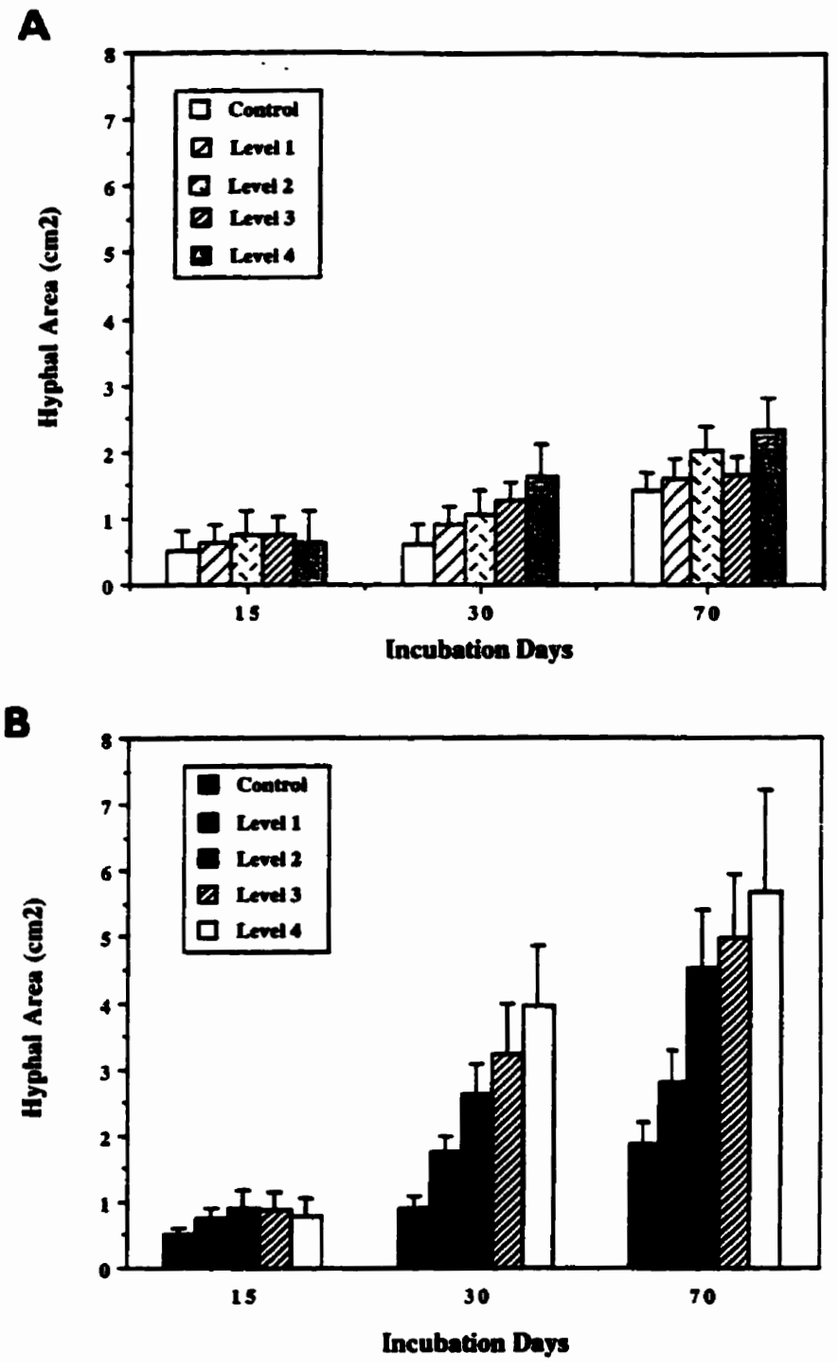

Fig. A and B. Effects of jack pine (*Pinus banksiana*) pollen treatment on ectomycorrhizal fungal growth (*Suillus brevipes*). Control = no pollen added; level 1 = 1.56 mg of jack pine pollen / plate (55 cm^2); level 2 = 6.25 mg; level 3 = 25 mg; and level 4 = 100 mg. (**Fig. A** no carbon substrate added to water agar medium; **Fig. B** 10 g/l of dextrose was added as carbon substrate).