THE UNIVERSITY OF MANITOBA

FIRE AND WOODLAND CARIBOU (RANGIFER TARANDUS CARIBOU): AN EVALUATION OF RANGE IN SOUTHEASTERN MANITOBA

by

James Allan Schaefer

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

ZOOLOGY DEPARTMENT

WINNIPEG, MANITOBA
February, 1988

ISBN 0-315-44118-6

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ABSTRACT

FIRE AND WOODLAND CARIBOU (RANGIFER TARANDUS CARIBOU): AN EVALUATION OF RANGE IN SOUTHEASTERN MANITOBA

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The effects of fire on the Aikens Lake population of woodland caribou were studied over a two-year period. Quantity, quality, and accessibility of forage were determined in recently-burned (5-year old) habitats, and compared to those in intermediate (37 year) and old-growth (90 - 160 year) condition. These measures were correlated to patterns of habitat utilisation by Aikens caribou over two winters.

Forage productivity was determined by harvesting current growth of vascular plants and biomass of lichens. Quality of forage was inferred from content of acid detergent fibre and published digestibility studies of *Rangifer*. Accessibility of forage was estimated from the Värriö Snow Index (VSI), and from intersection frequency of windfallen trees.

Burned habitats have suffered a decline in the quality and accessibility of winter forages due to the loss of *Cladina* lichens, the increase in snow thickness and hardness, and the accumulation of deadfalls. The oldest stands (160 years) showed decreased forage abundance but the most favourable nival conditions. Aikens caribou exploited the remnant lichen supply within the burn, but abandoned burned range in late winter; a synergistic effect between the accumulation of snow and deadfalls is implicated. This behaviour can be modelled with an index that combines VSI and deadfall frequency.

Taiga is not suitable for woodland caribou in its recently-burned and intermediate stages (up to 50 years following fire). Yet fire may be necessary to maintain optimal, long-term lichen resources. Woodland caribou adapt to the short-term detriments, which may not be fully realised until 5 years or more, by abandoning their range. Therefore access to alternative, lichen-rich stands is imperative.

ACKNOWLEDGEMENTS

This project benefitted immeasurably from the advice, assistance, and encouragement of others. William O. Pruitt, Jr., my supervisor, provided impetus for the study and guided it throughout. Members of my committee offerred invaluable advice on study design, analysis, and presentation. Wolf Heck advised me on the figures.

My sojourn at Taiga Biological Station was enhanced by many volunteers whose company I enjoyed and whose field work was both enthusiastic and proficient. Undergraduates from the University of Manitoba and members of the Manitoba Naturalists Society aided in lichen sampling and in ground searches. In particular, I am grateful to Mitch Campbell and to Dale Chapman for their plant harvesting abilities, and to Rogier Gruys for his deadfall-walking accomplishments. The companionship of volunteers, as well as of Bill Conley, resident of Wallace Lake, and Bill Brown, fellow graduate student, lifted the spirits and provided my fondest memories of 'Taiga'.

This study was supported financially by the World Wildlife Fund, the Taiga Biological Station Research Trust Fund, the Northern Studies Committee, and the Manitoba Department of Natural Resources. While at Taiga Biological Station I was supported by a University of Manitoba Post-Graduate Fellowship, and a Natural Sciences and Engineering Research Council Postgraduate Scholarship.

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1. INTRODUCTION

The view that fire is a natural part of the taiga ecosystem has recently found substantial support in the literature (Heinselman 1973, Johnson and Rowe 1975, Kelsall et al. 1977, Alexander and Euler 1981). Although these reports agree that taiga plant communities are fire-adapted or even fire-dependent, the effect of fire on caribou (*Rangifer tarandus*) and their habitat remains a contentious issue.

Early investigations, both of woodland caribou (*R.t. caribou*) and of barren-ground caribou (*R.t. groenlandicus*) on their taiga range, tended to stress the negative impact of fire: the decline of caribou was seen to be a result of the destruction of climax forest, particularly of its associated stands of forage lichens (Edwards 1954, Leopold and Darling 1953, Cringan 1956, Scotter 1964, Peterson 1966). Arboreal and terrestrial lichens, deemed essential in the diet of *Rangifer*, may require as long as 100 years to recover to pre-fire levels of abundance (Scotter 1971).

More recent investigations have questioned this thesis. Bergerud (1974a) dismissed wildfire as a possible cause for the decline, and claimed lichens were not essential in the caribou diet. Johnson and Rowe (1975) and Miller (1976, 1980) reached similar conclusions for barren-ground caribou in their taiga habitat. Moreover, these authors (agreeing with Ahti and Hepburn 1967) contend that fire may improve the quality of caribou range: fire may promote habitat diversity (by producing a mosaic of stands at several ages) and enhance lichen abundance (by removing the carpet of mosses typical of older stands).

The consequences of fire in the taiga are potentially more severe for the forest-dwelling subspecies of Rangifer, year-round inhabitants of this ecosystem. Recent advances in the nutritional relations of cervids and their ranges (White et al. 1975, Parker et al. 1984, Hobbs and Swift 1985) permit interpretation of the effects of fire from a dietary and energetic viewpoint. This has not been done for woodland caribou.

This study is concerned with the effects of fire on the habitat of a known population of woodland caribou, the Aikens Lake population in southeastern Manitoba. This research stems from the 1980 Wallace Lake fire, and from two studies of Aikens caribou prior to its occurrence (Stardom 1977, Darby 1979), and complements a recent investigation into the population's immediate post fire status, structure, and patterns of habitat utilisation (L.A. Decker, in preparation).

1.1 The Evaluation of Range

Any appraisal of habitat, Moen (1973: 26) wrote, ".... requires the recognition of those things that relate to the organism under consideration." For *Rangifer*, investigations have, for the most part, focussed on the abundance of forage, particularly of lichens (Cringan 1956, Ahti 1959, Scotter 1962, Ahti and Hepburn 1967, Pegau 1968, 1972, Bergerud 1972, Lindgren et al. 1983, Parker 1975 and references therein [p. 51]). Skoog (1968) and Bergerud (1974a) have criticised the preoccupation with lichens and the concept that lichens dictate carrying capacity of the range. Their arguments stem from the versatile food habits of *Rangifer* and from the weight loss incurred by animals on an *ad libitum* diet of lichen.

Assessments of the impact of fire on caribou habitat have largely parallelled other range studies emphasising food quantities. Scotter (1964, 1970, 1971) measured the standing crop of forages in an array of forest classes in northern Saskatchewan; the total standing crop of lichens and vascular plants was positively related with time since burning. Bergerud (1971), however, found that in Newfoundland the recovery of evergreen shrubs was rapid following fire (abundant at 6 years) and thought fire would enhance lichen abundance in closed-canopy forests. Miller (1976, 1980) established that lichen quantities are maximal in intermediate-aged stands in northern Manitoba.

Recent investigations into the value of Rangifer forage plants (Person et al. 1975, 1980a,b, White et al. 1975, Thomas and Kroeger 1980, 1981, Boertje 1981) permit evaluation of habitats on a nutritional basis. The interactions of forage quality and quantity are essential to understanding ruminant-habitat relations, but have not been applied in assessments of burned-over caribou habitat. Similarly, associations between woodland caribou and their range have received greater attention in recent years (Stardom 1975, Fuller and Keith 1981, Boonstra and Sinclair 1984, Edmonds and Bloomfield 1984, Darby and Pruitt 1984); yet intensive documentation of use by caribou in relation to fire-dependent features of habitat is generally lacking.

The absolute amount of food is an obvious, crucial factor in the ecology of Rangifer; yet the literature is replete with assertions that accessibility to forage, particularly due to the effects of snowcover ('api'), is a major determinant of overwintering behaviour (Pruitt 1959, Henshaw 1968, LaPerriere and Lent 1977, Miller 1974, Stardom 1975, Bergerud 1974c, Skogland 1978, Helle 1984, Russell and Martell 1984). Yet, despite the significance of snow in the ecology of caribou, and Pruitt's (1959) suggestion that nival parameters should be compared in burned and unburned ranges, this so-called 'indirect' factor has largely been ignored.

Downed trees that result from a fire also may restrict caribou from potential forages. Banfield (1954) found animals were deflected by recent burns during migrations. Scotter (1971: 222) noted that fire converts upland habitats into a 'tangle of fallen snags'. Stevens and Storey (1980) devised a subjective index for windfallen tree density for woodland caribou habitat assessments in Manitoba. This apparently salient factor has received only passing mention in the literature and is in need of clarification.

This report deals with an appraisal, in a nutritional and energetic context, of the effects of the 1980 Wallace Lake fire on the Aikens Lake range. Estimates of forage quantity, quality, and accessibility are made to assess the relative capacities of taiga habitats to support caribou. Comparisons of recently-burned, intermediate, and mature stands (Table 1), and of their relative use by caribou, are emphasised in an effort to distinguish between immediate, medium, and long-term implications for Aikens Lake caribou.

Table 1. Age classification for stands in the Wallace-Aikens study area.

Classification[a]	Date of Most Recent Fire	Age of Stand at Time of Study
burned	1980	4 - 5.5 years
burned	1976	8 - 9.5 years
intermediate	1948	36 - 37 years
mature	1895 or earlier	89+ years

[a] Unless otherwise stated, 'burned' condition in the text refers to stands originating from the 1980 fire. 'Mature' stands are in old-growth condition and may not be of seral maturity.

2. STUDY AREA

The study area, covering about 1400 km^2, lies within the Northern Coniferous Section of the Boreal Forest Region (Rowe 1972). The region is dominated by Precambrian outcrops, up to 30 m in height, with numerous intervening poorly-drained sites and small lakes. Taiga Biological Station (TBS), located near Wallace Lake, was the base for field activities during the study (Figure 1). Road access and human activity are confined primarily to the southwestern part of the area, although prospecting, tourism, and rice harvesting occur throughout the region.

Climate is boreal continental, with mean January and July temperatures in the nearby town of Bissett -21 ^{o}C and +18 ^{o}C, respectively (Environment Canada 1982). Snowfall averages 171 cm annually; total rainfall is 434 mm per year.

Rainfall for the two summers (May to September) 1984 and 1985 was about normal (Figure 2), but 1984 saw a somewhat wet spring and early summer, while late summer was dry. Summer 1985 was the converse. Temperatures were close to normal in 1984, 2 C^{o} below normal in 1985. Snowfall was slightly below normal the two winters (November to March) 1984-85 and 1985-86. Significant accumulations arrived earlier during the second winter, however. Weather data are from the the Atmosphere Environment Service station at the town of Bissett (51^{o} 01'N, 95^{o} 40'W).

Figure 1. The Wallace-Aikens Lake study area.

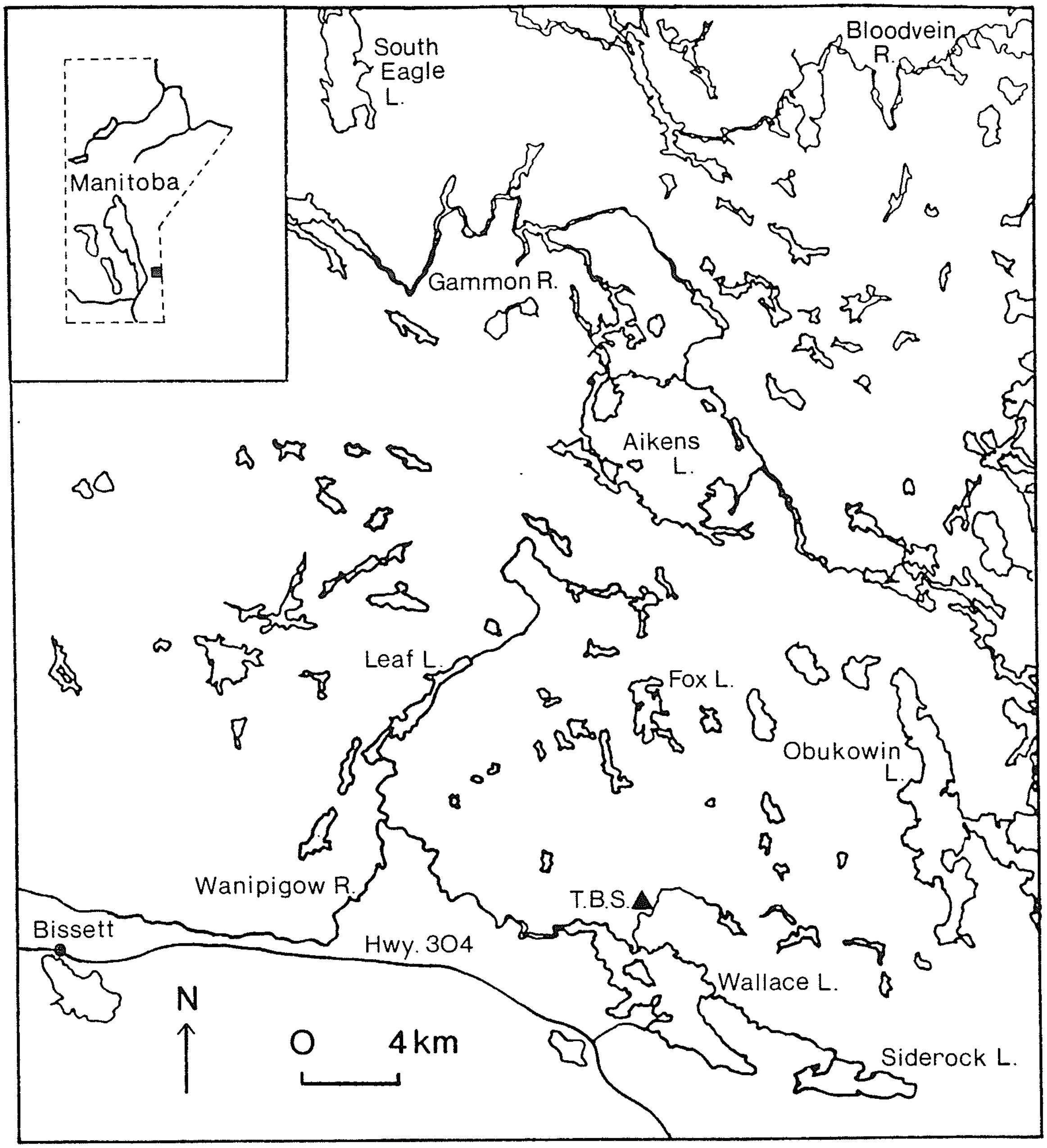
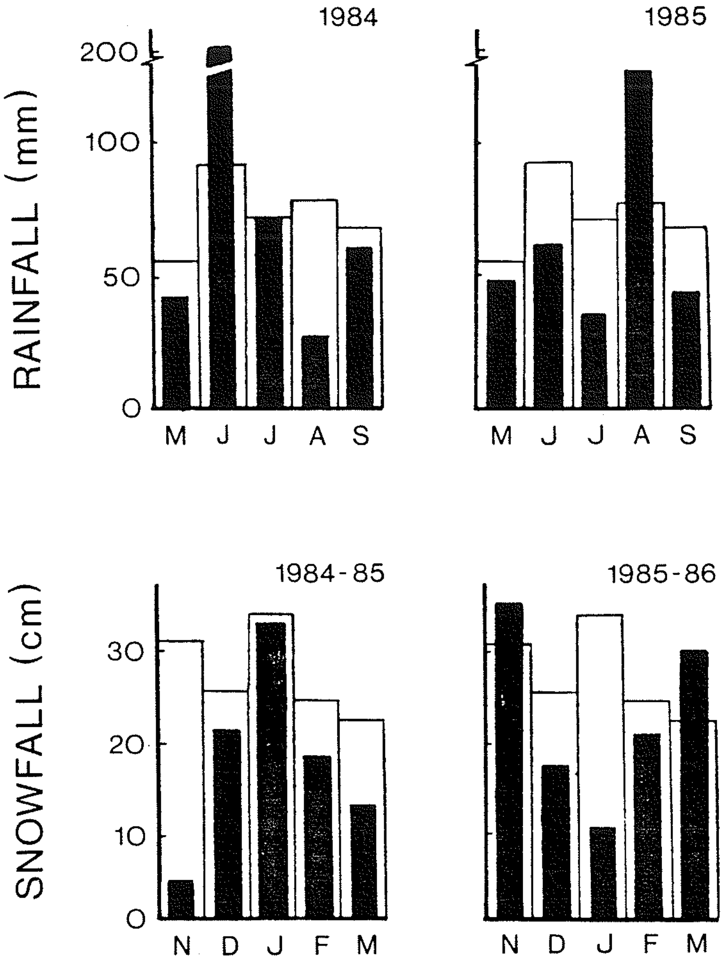

Manitoba
South Eagle L.
Bloodvein R.
Gammon R.
Aikens L.
Leaf L.
Fox L.
Obukowin L.
Wanipigow R.
T.B.S.
Bissett
Hwy. 304
Wallace L.
Siderock L.
N
0 4km

Figure 2. Monthly data from Bissett of rainfall (May to September) and snowfall (November to March) during field activities (solid bars) and normals (open bars).


1984
1985
RAINFALL (mm)
200
100
50
0
M J J A S
M J J A S
1984-85
1985-86
SNOWFALL (cm)
30
20
10
0
N D J F M
N D J F M

2.1 Aikens Caribou

Prior to 1970, studies of Aikens woodland caribou were limited to annual provincial aerial surveys. Stardom 1977:169) considered the only reliable estimate of population size during that period to be 46 animals, determined in December 1968.

In 1971 intensive research in the Wallace-Aikens Lake region began with Stardom's (1975, 1977) investigation into the animals' winter ecology, with emphasis on caribou responses to snowcover. He also conducted preliminary vegetation inventories, and assessed interrelationships with moose (*Alces alces andersoni*) and white-tailed deer (*Odocoileus virginianus*).

Darby (1979) provided baseline population characteristics from 1975 to 1977. Individual seasonal movements, herd structure and habitat use were monitored. Major findings are presented in Darby and Pruitt (1984). L.A. Decker (in preparation) began assessment of the 1980 fire by replicating aspects of these two baseline studies.

Estimates of population size are from several sources: 46 animals in 1968 (Stardom 1977), 35 to 37 from 1970 to 1972 (Stardom 1977), 30 to 35 in 1975 (Hill 1979), 30 to 40 from 1975 to 1977 (Darby 1979), and 35 in 1984 (L.A. Decker, personal communication). Aikens caribou apparently have never existed at high densities, and, at least for the past

15 years, have maintained a stable population size even immediately after the 1980 fire.

2.2 Wallace Lake Plant Communities

Identification of potential caribou habitats was accomplished from a stratified vegetation map, made one year prior to the 1980 fire (unpublished TBS files). Classification was based on drainage conditions and overstory, identified from 1:15,840 black and white aerial photographs, and on understory confirmed by ground truthing. Extent of the map, bounded by Siderock, Leaf, Obukowin and Aikens lakes, approximated pre-fire Aikens caribou range.

Five major habitats are recognised, with further subdivisions on the basis of canopy closure. Except for bog habitats, however, these subdivisions were disregarded. This simplification was desired for two reasons: (1) Reduction in the number of recognised habitats simplifies analysis of habitat selection (Alldredge and Ratti 1986); (2) Canopy closure of a given site is largely an age-related phenomenon and comparison of taiga habitats at various ages was the main objective of study; stands of the same subtype tend to fall into the same age / habitat class anyway.

The study area, therefore, was partitioned into 4 upland and 5 bog communities. The following is a brief description of each type, with a summary in Table 2. Nomenclature follows Hale (1979) for lichens, Conrad (1959) for mosses, and Scoggan (1978) for vascular plants. (Quantitative details of understory and canopy are in Appendices A and B, respectively.)

Mature bog (1a): This is a mature spruce bog community dominated by large, closely-spaced black spruce (Picea mariana) trees. The moss layer is interspersed with both Sphagnum and feather mosses (Dicranum sp., Hylocomium splendens, Pleurozium schreberi), reflecting the drier nature of the bog habitat. Ledum groenlandicum, Vaccinium vitis-idaea are the dominant ericoids, although mats of Oxycoccus sp. or Gaultheria hispidula may occur.

Intermediate bog (1b): This bog is similar to the mature (1a) type but is wetter and more open. Black spruce remains the dominant tree but tamarack (Larix laricina) often makes a significant contribution. Kalmia polifolia and Chamaedaphne calyculata now occur with Ledum as dominant shrubs. Smilacina trifolia and graminoids are more frequent than in 1a communities.

Bog-forest (1d): This appears to be a transitional community characterised by large, widely-spaced tamarack, black spruce, and occasional aspen (Populus sp.). The understory is often choked with alder (Alnus spp.) and willow (Salix spp.). Sphagnum hummocks support a wide array of shrubs (Ledum, Chamaedaphne, and V. vitis-idaea), forbs

Table 2. Floral characterictics of the study area habitats in mature (90+ years) condition.

	Community Type[a]	Dominant Understory Species
1a	mature bog	Ledum groenlandicum, Vaccinium vitis-idaea, feather mosses, Sphagnum spp.
1b	intermediate bog	Chamaedaphne calyculata, Kalmia polifolia, Ledum, Sphagnum spp.
1c	uncommon bog	(not studied)
1d	bog-forest	Alnus spp., Ledum, Sphagnum spp., feather mosses
1e	semi-open bog	Chamaedaphne, Kalmia, Andromeda glaucophylla, Sphagnum spp.
1f	sedge meadow	Salix spp., Myrica gale, Alnus spp., graminoids
2	jackpine forest (i.e. sandplain)	Arctostaphylos uva-ursi, V. vitis-idaea, Vaccinium spp., Linnaea borealis
3	mixed coniferous forest	Cornus canadensis, Maianthemum canadense, Coptis trifolia, Lycopodium spp., feather mosses
4	jackpine forest (i.e outcrop) with intervening black spruce bog	Cladina rangiferina, A. uva-ursi, Vaccinium sp., Potentilla tridentata
5	mixed deciduous-coniferous forest	Cornus canadensis, Diervilla lonicera, Clintonia borealis, Linnaea borealis

[a] Jackpine forest (habitat 2) is most frequently found in the form of an outcrop, similar to habitat 4.

(Smilacina trifolia, Trientalis borealis), and grass-like plants.

Open bog (1e): This type is characterised by stunted, well-spaced black spruce and tamarack over Sphagnum hummocks. Free-standing water may occur. The ground flora is dominated by ericaceous shrubs, Ledum on drier patches and Chamaedaphne, Kalmia, and Andromeda glaucophylla in the hollows. Oxycoccus, grasses, and sedges are also common, and Betula glandulosa is an occasional shrub.

Sedge meadow (1f): This is a hydric community lacking mature trees but abundant in Salix, Alnus, Betula, and Myrica gale. There is a lush cover of grasses and sedges, but Potentilla palustris is one of few forbs.

Jack pine forest (2): This type, dominated by jack pine (Pinus banksiana), may occur on sandplains or outcrops. The latter are more common. Stands may be almost pure jack pine, although black spruce and birch (Betula papyrifera) make scattered representation. On outcrops lichens (particularly Cladina rangiferina) and feather mosses dominate the ground flora. Amelanchier species, Vaccinium species, Juniperus horizontalis, and Arctostapylos uva-ursi are common shrubs, with Potentilla tridentata and Maianthemum canadense common forbs. On sand the abundance of Cladina lichens is reduced, while Vaccinium vitis-idaea, Linnaea borealis, and Chimaphila umbellata are more prevalent.

Mixed coniferous forest (3): This is a mature community consisting of white spruce (Picea glauca), balsam fir (Abies balsamea), and black spruce with occasional jack pine. There is a luxuriant carpet of feather mosses supporting a variety of forbs (Cornus canadensis, Aralia nudicaulis, Coptis trifolia, Maianthemum, and Trientalis). Shrubs are uncommon.

Jack pine forest with intervening black spruce bog (4): This community is a heterogeneous mixture of rock ridges interspersed with poorly-drained sites. The ridges are similar to habitat 2. The intervening bogs are primarily black spruce-dominated, similar to mature (1a) communities, although alder and birch may invade along the edges.

Mixed deciduous-coniferous forest (5): Here deciduous trees form 30 to 70 percent of the tree cover, along with occasional black spruce, white spruce, and balsam fir. The deciduous component may consist of trembling aspen (Populus tremuloides) or paper birch (Betula papyrifera). The understory is diverse but Diervilla lonicera, Vaccinium species, and Linnaea borealis are the most common shrubs. Cornus canadensis, Maianthemum, Aralia nudicaulis, Rubus species, Fragaria species, and Clintonia borealis are part of a wide array of forbs. Feather mosses dominate the ground layer but leaf litter is usually abundant.

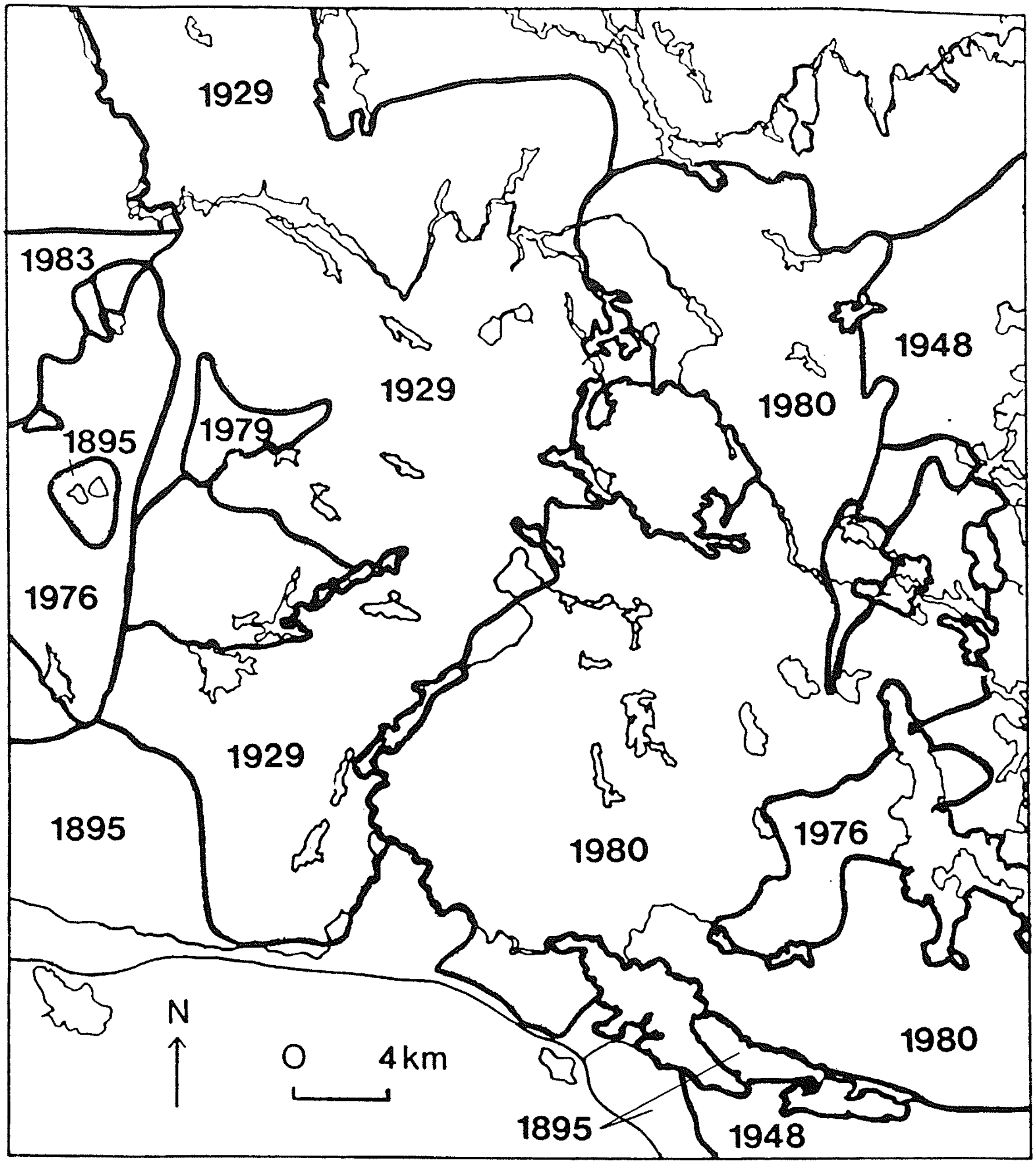
2.3 Fire History and Characteristics

The prevalence of jack pine through most of the Wallace-Aikens region is a testament to the occurrence of wildfires for at least the past century. Cayford and McRae (1983) review the adaptations of Pinus banksiana to fire: cone serotiny, high seed retention on the tree, rapid seed dessimination and germination following fire, and high light tolerance of seedlings make the species highly-adapted to fire. Indeed, these authors consider burning to be 'an indespensible phase in the natural life cycle of jack pine'; the species would eventually be supplanted by more shade-tolerant trees if fire was excluded from the taiga (Day and Woods 1977).

Figure 3 presents the approximate extent of fires for most of the study area; the map was extracted from 1982 aerial photographs, Stardom (1977), Darby (1979), and unpublished files from Abitibi-Price Limited and Taiga Biological Station.

Prior to 1975, the range was essentially composed of stands resulting from fires during 1895 (bounded by Fox, Aikens, Wallace and Obukowin lakes), in 1929 (to the west of Fox and Aikens lakes) and in 1948 (south and east of Obukowin Lake). In 1976, a lightning-initiated fire consumed 40 km^2 of 81-year-old timber. The 1980 fire was man-caused and covered approximately 600 km^2 of both 85-year-old and 51-year-old forest. The extent of these two

Figure 3. Distribution and year of occurrence of fires for most of the study area.

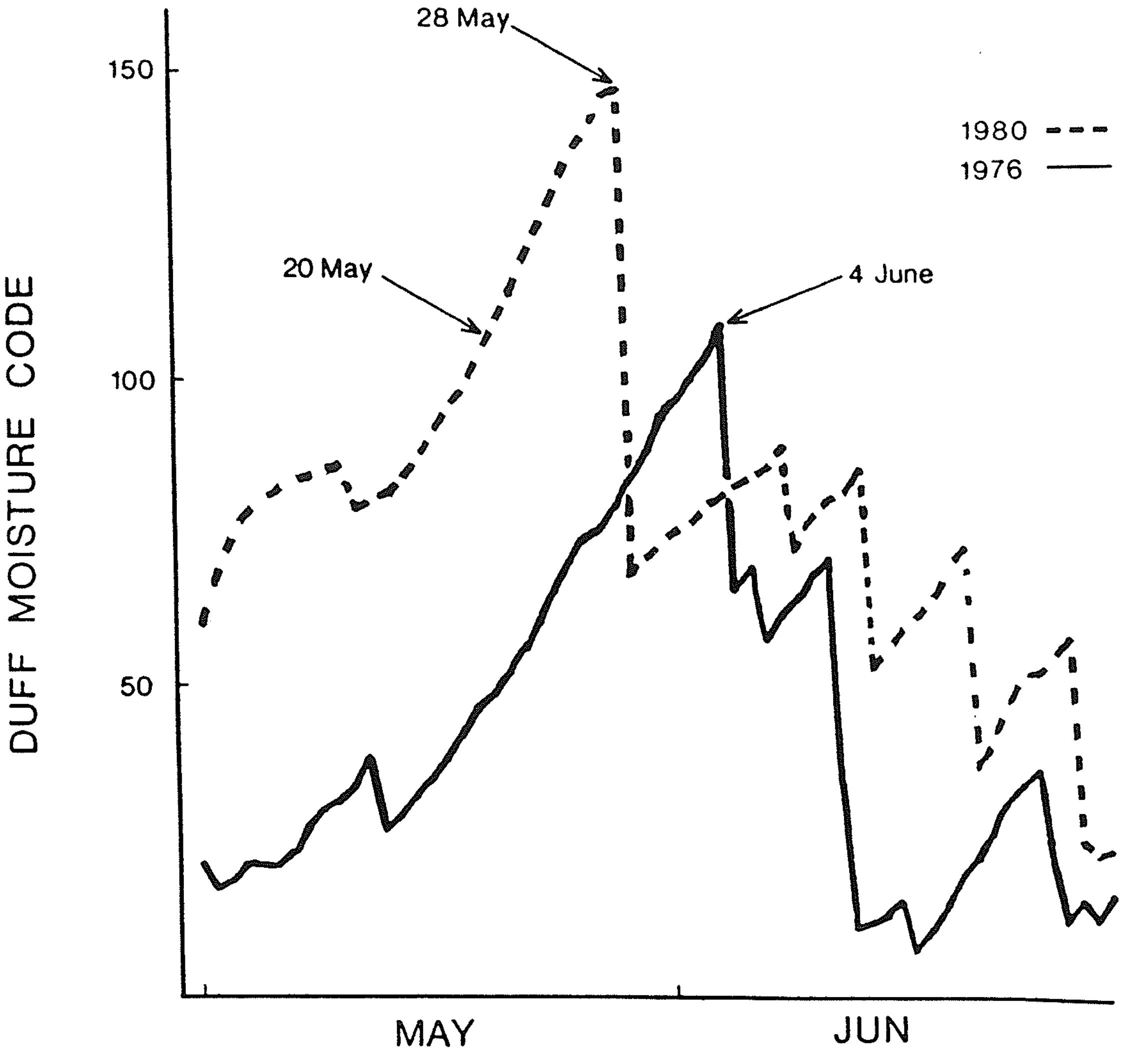

1929
1983
1929
1980
1948
1895
1979
1976
1929
1895
1980
1976
N
0
4 km
1980
1895
1948

most recent burns is nearly mutually exclusive: the author has noted only small 'double-burned' pockets near Little Caribou, Steepside and Obukowin lakes.

Consumption of the organic layer of soil by fire is an important determinant of revegetation, particularly for jack pine (Cayford 1971, Ohmann and Grigal 1981, Cayford and McRae 1983, Van Wagner 1983). Depth of burn is largely independent of fire intensity, but is correlated with the Duff Moisture Code (DMC) of the Canadian fire danger system (Canadian Forestry Service 1984). Data from CFS, Winnipeg branch, indicate that at time of ignition, the 1976 and 1980 fires were nearly identical in DMC (Figure 4). Their respective values of the Build-up Index (BUI) (of which DMC is a component) are correspondingly similar (108.8, 108.2). In 1980, however, the wildfire continued to burn until 28 May at low moisture levels. Heavier post-fire rains in 1976 seem to have contributed to higher soil erosion, and greater jack pine regeneration at the expense of potential forage species (personal observation). Both these fires had significantly higher values of DMC and of BUI than the Lesser Slave Lake fire in Alberta (Alexander 1983) or two northern Ontario burns (Walker and Stocks 1972); in the latter case, consumption of organic soil was substantial, and jack pine regrowth high (Methven et al. 1975).

The behaviour of wildfires is not random, however, and topography often dictates fire spread and intensity (Nordin and Grigal 1976, Johnson 1979). While many areas burn

Figure 4. Daily values of the Duff Moisture Code during the 1976 and 1980 fires. 20 May and 4 June were ignition dates. (Data courtesy of the Canadian Forest Service).


28 May
20 May
4 June
1980
1976
150
100
50
DUFF MOISTURE CODE
MAY
JUN

repeatedly, others remain extremely resistant to combustion. This is particularly true of poorly-drained bogs within the study area (Stardom 1977, Darby 1979). To quantify this effect, 454 Universal Transverse Mercator (UTM) grid intersection points (1 km apart), projected onto 1:15,840 post-fire (1982) aerial photographs, were interpreted. Points were classified as unburned, burned in 1976, or burned in 1980. Because only canopy was considered, surface-only fires were undetected and thus 'unburned' areas may be overestimated; however, more than two years of extensive ground investigations within the study area indicate that surface fires occur only in small, isolated patches.

Table 3 indicates that about one-third of the area within both recent burns remains intact. This resistance to fire, however, is strongly habitat-dependent: apparently all semi-open bogs (1e) survived while nearly all upland communities burned. Mixed decidious-coniferous forests (habitat 5) may be less susceptible than other upland communities to the fire due to their more mesic nature; note, however, their absence from the area burned in 1976.

It is noteworthy that another major wildfire swept through the taiga habitat south, east, and northeast of Wallace and Siderock Lakes in May 1987. Officially, the cause of the fire was undetermined.

Table 3. Habitat type composition (percent) of the Wallace-Aikens study area. Blanks represent zeros.

Community Type	Unburned	Burned 1976	Unburned Within 1976 Burn	Burned 1980	Unburned Within 1980 Burn	Totals
Bog Communities						20.1
mature 1a	0.2			1.5	2.0	3.7
intermediate 1b	0.7		0.7	0.9	4.6	6.8
uncommon 1c	0.2					0.2
bog-forest 1d	0.2			0.4	0.7	1.3
semi-open 1e	0.7		1.3		6.4	8.4
sedge meadow 1f	0.2				0.4	0.7
Upland Communities						68.8
jack pine sandpln 2	0.6	0.4		2.8		3.8
jack pine outcrop 2	3.5	3.1		21.8	1.2	29.8
mixed coniferous 3	0.9	1.3		4.2		6.4
jack pine outcrop 4	1.8	2.2		13.9		20.0
intervening bog 4		0.4	0.2	0.4	1.1	2.2
mixed deciduous 5	2.9			3.1	0.7	6.6
open water						12.1
Totals	11.9	7.5	2.2	49.0	17.1	100.0

3. METHODS

3.1 Vegetation Survey:

3.1.1 Ground Investigations

An extensive survey of vegetation was performed to provide quantitative estimates of the composition of Wallace Lake plant communities, test the original classification, and ensure agreement with sites chosen for productivity estimates. Community data were ordinated (Pielou 1984) to aid in these objectives. Emphasis was placed on upland habitats due to their apparently greater variability of composition and susceptiblity to fire, and on the plant species that comprise potential caribou forages.

All sampling occurred between 12 June and 31 July 1985 in an 'accessible' region. The limits of the sampling region were defined as 0.5 km from established summer trails, and 1.0 km from Wallace Lake, Obukowin Lake, Wanipigow River, and Provincial Highway 304. Sampling was conducted within these limits; islands were excluded.

Within this region, discrete areas of the four upland types were selected at random; allocation was approximately equal for each habitat x age combination. Minimum size of discrete areas was 1.0 ha. Once an area was chosen two sampling locations were picked randomly with help of 1:15,840 aerial photos and a grid overlay of points at 50 m intervals. Each of these locations selected is referred to as a 'site'.

At each site a 50 m 'main transect' was established. Its exact origin was determined by the toss of a stone, its orientation (north or south) by the toss of a coin. At three random points along the transect, a 'branch transect' was established with a random east or west direction. Six quadrats, 20 cm x 50 cm, were placed longitudinally at random 1 m intervals along the branch transect. Thus each site comprised 18 0.1 m^2 quadrats.

At each quadrat the number of current year's shoots of forbs and shrubs emerging above the moss layer within the quadrat was recorded. Shrubs were sampled up to a height of 2.0 m. Such a sampling regime using density rather than ocular estimates is perhaps more time-consuming, but was preferred here because of its objectivity and relative insensitivity to temporal change. Each site required about 1.5 hours to sample, apart from travel time.

Plant species not amenable to density measurements were assigned to one of 6 unequal cover classes as suggested by Daubemire (1968):

class	estimated cover (%)
I	0 - 5
II	5 - 25
III	25 - 50
IV	50 - 75
V	75 - 95
VI	95 - 100

Such species included the mosses, lichens, graminoids, *Gaultheria* species, *Linnaea borealis*, *Marchantia polymorpha*, and *Oxycoccus* species. The mid-point of each cover class was used in statistical analyses.

Overstory composition was noted at each quadrat. A circular plot of radius 2.0 m around the transect point was visualised and the number of stems of trees (at least 2.5 m in height) was recorded. In burned areas these data represent the pre-fire canopy structure.

Bog habitats (type 1) were sampled in a similar fashion. Discrete areas were chosen from the vegetation map solely on the basis of accessibility, and only 4 quadrats were analysed per branch transect. Thus each site is represented by 12 rather than 18 plots.

Occasionally, ground truthing was used to reclassify habitats. A list of these amendments was submitted to TBS files. In all, 1440 quadrats from 82 sites were analysed.

3.1.2 Vegetation Aerial Survey

A single flight was conducted on 29 April 1986 to locate lichen-dominated outcrops within recent burns. These areas had suffered crown-only fires, leaving ground vegetation intact.

Procedure was modified from caribou aerial surveys (see Caribou Aerial Surveys, Section 3.5.1): flight lines were confined to the 1976 and 1980 burns south of Aikens Lake, and were interspaced by 1.25 km to achieve 100% coverage. Sites with burned overstory but with intact lichen substrate were transcribed onto a 1:30,000 photo-mosaic. Total coverage of these areas was determined by a CalComp digitizer.

3.2 Forage Quantity:

3.2.1 Ground Vegetation

Productivity of vegetation of taiga plant communities was considered to approximate best the absolute abundance of forage for caribou. Because grazing capacity is based on sustained yield, production rather than standing crop better reflects food availability, as well as better approximating in most cases the plant parts used by caribou. Thus production at peak biomass constitutes the basis for comparison of Wallace Lake habitats.

A harvest regime was conducted between 2 August and 8 September 1985. Pre-fire aerial photos, the stratified vegetation map, and ground truthing permitted selection of a 'typical' site of each of the recognised habitat types (Figures 5 and 6). Sites were chosen for their accessibility, typicalness, and conformity between analogues

Figure 5. Location of harvest sites for bog communities. Letters represent habitat sub-types. All sites were in 'mature' condition except the 1a bog site north of Wallace Lake which burned in 1980.

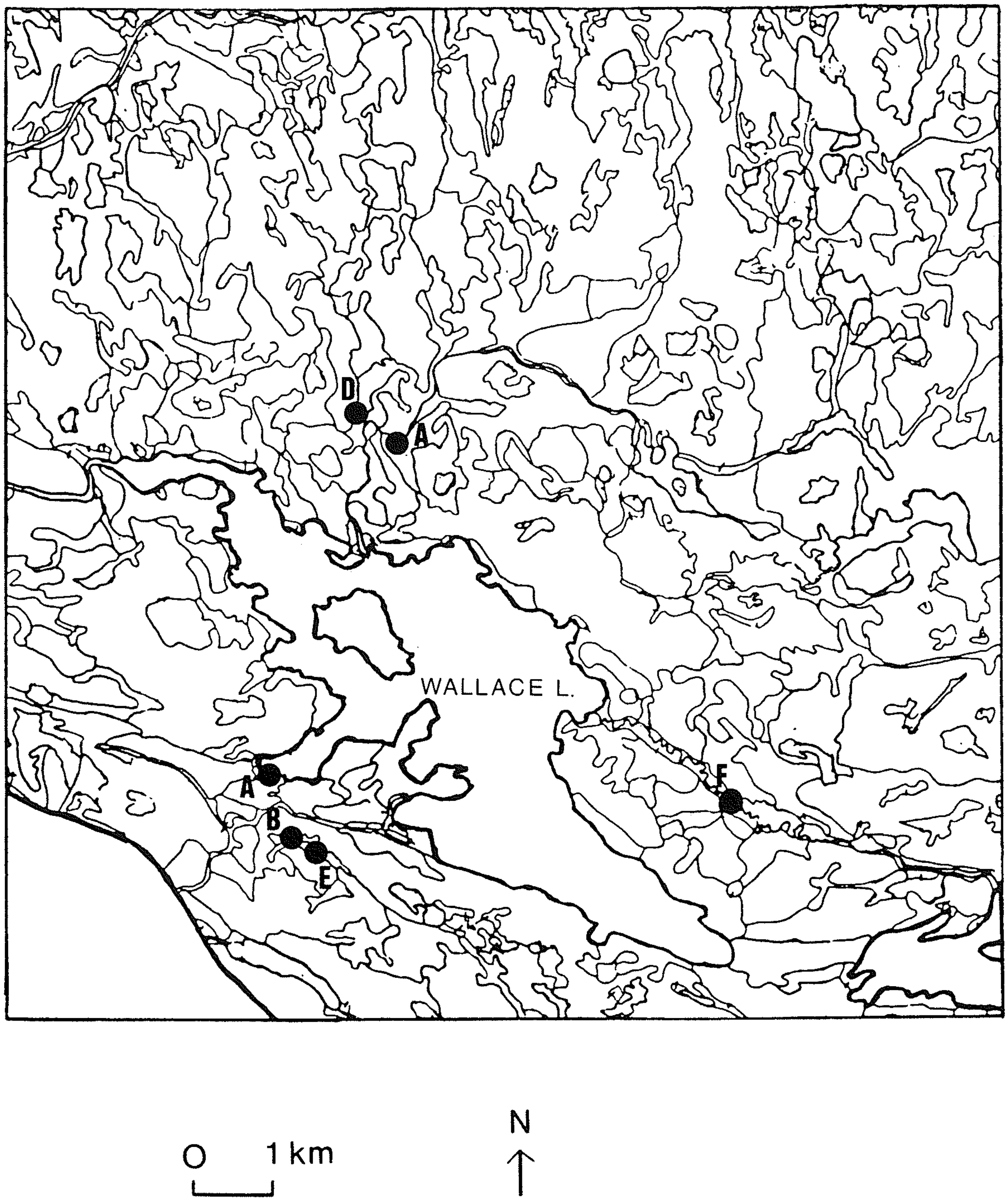
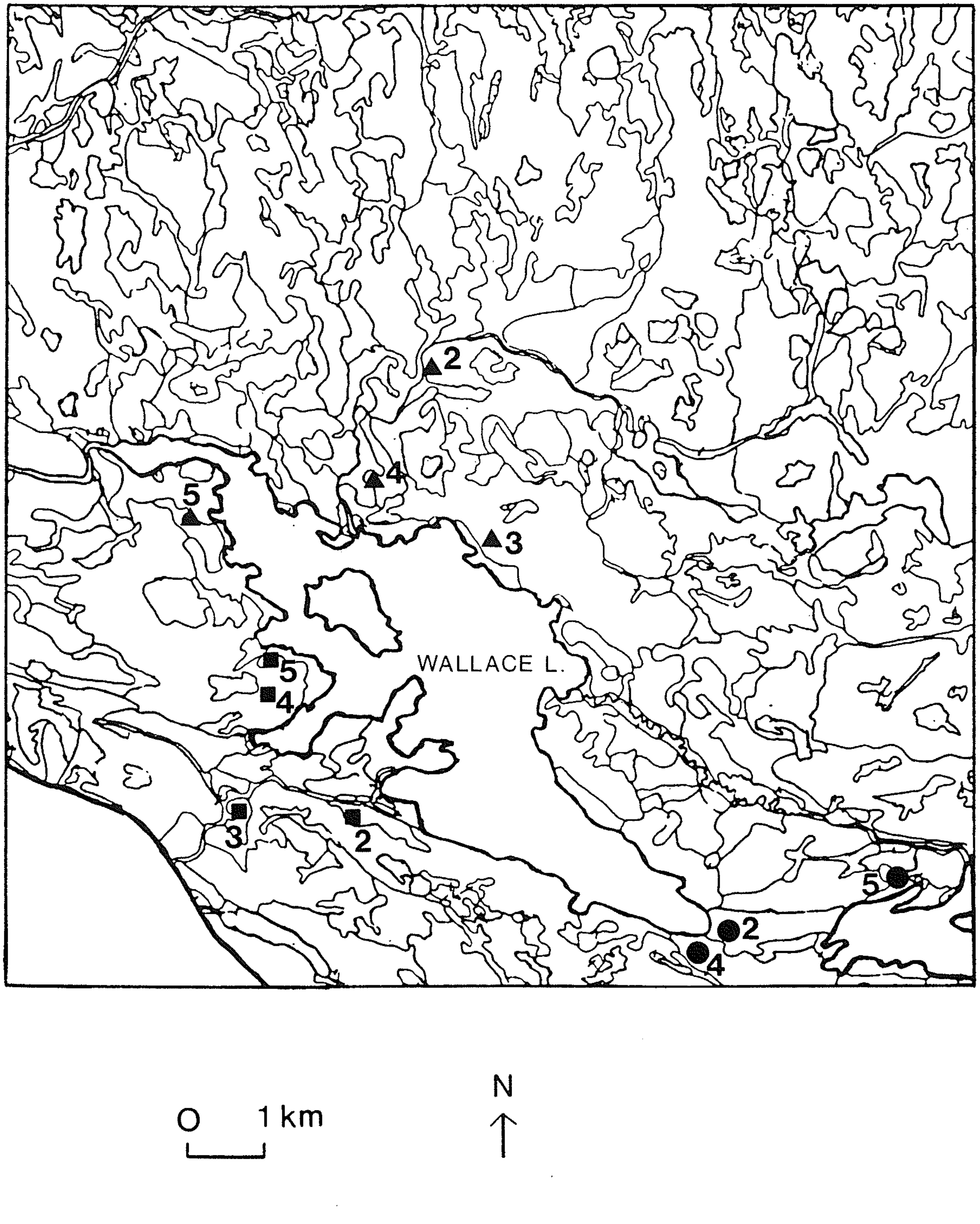

D
A
WALLACE L.
A
B
E
F
O
1 km
N

Figure 6. Location of harvest sites for upland communities in mature (squares), intermediate (circles), and burned condition (triangles). Numbers represent habitat types.


2
4
5
3
WALLACE L.
5
4
3
2
5
2
4
O
1 km
N

in canopy and ground vegetation. Following the procedures of Ritchie (1958), jack pine habitat (2) was further subdivided and was represented by a sandplain. At each site a 6 m x 50 m macroplot was established.

Sampling was carried out on rotating basis for each habitat type. Each macroplot was visited a total of 4 times. Analogues were, with one exception, sampled within 48 hours of one another.

At each visit, a 50 m transect was established within the macroplot along which 20 cm x 50 cm quadrats were placed at random 1 m intervals. Sampling effort was based on the perceived homogeneity of the habitats and time required to sample each: 20 quadrats per transect were clipped in upland sites, 15 in mature (1a) and intermediate (1b) bogs and bog-forest (1d), and 12 in semi-open (1e) and sedge (1f) bogs. At each subsequent visit the transect was shifted 2 m to the left or right.

Each quadrat was first treated in an identical fashion to those during the extensive vegetation survey: the number of new shoots was counted for each species emerging above the moss layer. Shrubs were sampled up to 2.0 m high. Plant species where density was impossible to measure were alloted to one of 6 unequal cover classes. (See Vegetation Survey, Ground Investigations, Section 3.1.1).

Plants were then harvested by removing the current year's growth of herbs and shrubs above the moss layer. Where current production could not be determined readily, as in the case of lichens, creeping shrubs (Gaultheria hispidula, Linnaea borealis, Oxycoccus species), and perennial herbs (Chimaphila umbellata, Lycopodium complanatum, and L. obscurum), the entire living portion of the plant was clipped; these data therefore represent live standing crop. Production of these species was estimated as 10 % of standing crop of lichens (Andreev in Davis et al. 1978) and 50 % of the above perennials, although this latter estimate requires verification.

Samples were permitted to air dry to constant weight, then weighed using Pesola scales to the nearest 0.1 g. Samples over 4.0 g were weighed to the nearest 0.5 g. Lichens were cleaned of litter and the decadent lower portion, then, due to their hygroscopic nature, were dried at 60 °C for 8 hours before weighing. Plants submitted to the Feed Analysis Section (Manitoba Department of Agriculture) indicated that samples contained 19.1 % moisture (std = 3.9%). Thus dry matter weight of all plant samples was determined by multiplying by a coefficient of 0.809 .

To aid in the quantitative description of each site, canopy structure was determined by counting trees (greater than 2.5 m in height) within the macroplot expanded by 2 m along each long border (hence a 10 m x 50 m plot).

Time required to clip and sort plants from each transect (usually 20 x 0.1 m^2 plots) averaged about 6 hours for one person. This effort varied considerably depending on the abundance and diversity of species at a given site. Separation of lichens from litter proved time-consuming where cover exceeded 50 percent in a quadrat. In all, 1224 plots were analysed.

To test the original stratification of Wallace Lake habitats and to verify that harvest sites were representative, an ordination was performed. Principal components analysis (PCA) (SAS 1982) was carried out on the density of understory species from these typical plots and those from the extensive vegetation survey. Because density is qualitatively different for each plant species, the data were standardised using a correlation matrix (Pielou 1984). Rare species (frequency < 3 for each age class) were eliminated from the analysis.

3.2.2 Arboreal Lichens

A separate sampling regime was followed to estimate the abundance of arboreal lichens. Only intermediate (1b) and semi-open (1e) bog habitats were considered. Closed bogs (1a, 1d types) and upland habitats were excluded because their available arboreal lichen biomass, as a result of inaccessibility of the overstory, was considered to be negligible. Sampling procedure was modified from Van Daele and Johnson (1983).

Seven discrete bog habitats (three intermediate 1b and four semi-open 1e sites) were selected on the basis of accessibility and sampled between April 1985 and January 1986. Actual site location was determined randomly using a grid overlay on 1:15,840 aerial photographs. At this site a 20 m X 20 m plot was established.

Within each plot about 25 trees (> 2.5 m in height) were chosen haphazardly. All sampling occurred between 0.5 m to 2.5 m in height; a 2.5 m pole aided in stratifying each tree into sampling intervals. First the number of branches (> 20 cm in length) was tallied in a random 0.5 m segment; then 2 branches were harvested from a random 0.1 m interval. If more than 2 branches were contained in a harvesting interval, the two closest to the lower boundary were selected. In addition, lichens on the bole closest to these branches were removed.

Lichens were separated from debris in the laboratory, dried for 8 hours at 60 °C and weighed to the nearest 0.1 g. The estimated biomass of lichens ($g \cdot m^{-2}$) was calculated by the formula:

$$\frac{\text{mass of lichen}}{\text{2 branches}} \times \frac{\text{mean no. of branches}}{\text{segment}} \times \frac{\text{4 segments}}{\text{tree}} \times \frac{\text{no. of trees}}{400\ m^2}.$$

3.3 Forage Quality

For cervids, acquisition of energy is viewed as the primary nutritional demand, particularly during winter (Moen 1973, Mautz 1978). Because energy value of forages is closely linked to digestibility for ruminants (Van Soest 1982, Robbins 1983), quality of taiga forages can largely be equated to their respective digestiblities.

With the exception of lichens, estimates of dry matter digestibility (DMD) of many woodland caribou forages are currently unavailable. Hence the DMD of Wallace Lake plants could not be determined directly, but was inferred from two sources: (1) published values of digestibility of forages for Rangifer; and (2) the relationship between digestibility and acid detergent fibre (ADF), an analytical component of feedstuffs.

Several studies have been concerned with the nutritional value of caribou diets in North America (Person et al. 1980a,b; Thomas and Kroeger 1980, 1981; Boertje 1981). I compiled a list of forage species from these sources and others, together with reported estimates of digestibility (in vitro dry matter disappearance [IVDMD] or nylon bag digestibility [NBD or in situ]), and ADF composition. Additional digestibility trials of lichens (McEwan and Whitehead 1970, Wales et al. 1975) were included. Plant species were categorised by growth form and by season of collection ('summmer' = May to September, 'winter' = October to April). Samples consisting of mostly senescent tissue during the summer period were placed in the 'winter' season.

Where possible, digestibility estimates for shrubs were based on NBD rather than IVDMD. Person et al. (1980b) suggest that the *in vitro* system fails to model the rumen adequately for these groups due to the accumulation of toxic inhibitors, and similarly, Kuropat and Bryant (1983) found a negative relationship between phenolic content and IVDMD. Person and colleagues' *in vitro* measures for shrubs were 26 to 46 % lower than those obtained *in situ*. The compiled list of estimates from the above sources, excluding Person et al. (1980b), indicates that the median summer IVDMD for deciduous shrubs (n = 28) was 12 % lower than that for NBD; for evergreen shrubs it was 10 % lower (n = 6). Since estimates for these two groups during winter are based solely on IVDMD, the predictions may represent underestimates.

In vitro procedures may also be inadequate for determining the digestibility of lichens, apparently due to nitrogen deficiencies (Person et al. 1980b). IVDMD data where authors suggest such limitations (i.e. Person et al. 1980b, Thomas and Kroeger 1981) were excluded. In addition, lichens were not recognised by season due to their apparent insensitivity to temporal change. The estimated DMD for lichens of 62 % is within, but perhaps at the low end of, in vivo DMD for lichens (56 to 72 %), the only in vivo determinations of any caribou forages (White et al. 1981).

Acid detergent fibre is an analytical, and largely indigestible fraction of the plant consisting of lignin, cellulose, and some ash. The inverse relationship between ADF and DMD is well documented for domestic ruminants (Van Soest et al. 1978, Minson 1982). Data from Rangifer nutritional studies are consistent with this relationship (White et al. 1975, Kuropat and Bryant 1983).

Plants harvested from clip plots were retained for determination of content of ADF and other nutrients (Appendix E). Analyses were performed by the Feed Analysis Section of the Manitoba Department of Agriculture (Winnipeg) following the methods of the Association of Official Analytic Chemists (AOAC, 1984). Crude protein was determined by Kjeldahl analysis, calcium (Ca) by atomic absorption, phosphorus (P) by photometric analysis, and ADF by the procedures of Goering and Van Soest (D. Waddell, personal communication).

These two sources, published digestibility values and measured ADF content, were used to generate reference equations for the DMD of Wallace Lake vascular plants (Appendix D). These estimates are based on the premise that (1) plants of similar growth form at similar times of the year tend to have similar digestibilities; and (2) ADF content negatively influences digestibility. Such an approach, although broadly-based, remains limited, and underlines the need for digestibility studies with woodland caribou.

Within each group / season, therefore, a reference equation relates the ADF content of study area plant groups to digestilities reported in the literature (Table 4). For lichens, graminoids, winter forbs, and less abundant species not submitted for chemical analysis, simply the median was applied.

3.4 Forage Accessibility:

3.4.1 Api Conditions

Api (snow-on-the-ground) conditions were monitored on an approximately biweekly basis from January to March following the methods of Pruitt (1959). A modified NRC kit was used. Stands of intermediate age (37 years) were ignored because their area represents only a minor fraction of the study area. Sampling was restricted to this time period since nival conditions prior to January were considered to have a negligible effect on caribou behaviour; by late March diurnal variations in hardness made habitat comparisons unreliable.

Sampling procedure differed slightly between the two winters. In 1984-85, biweekly sampling was allocated to all upland types and was alternated between mature (1a) and

Table 4. Estimation of dry matter digestibility (DMD) for study area plant groups. Reference equations relate reported DMD values with empirically-determined acid detergent fibre (ADF) content. Median values were applied to graminoids, lichens, winter forbs, and rare species not submitted for ADF determinations.

Season	Plant Growth Form	Median	Reference Equation
summer	deciduous shrubs	61.9	66.5 + 0.392 (22.5 - ADF)
	evergreen shrubs	56.2	64.4 + 1.151 (35.0 - ADF)
	forbs	69.0	75.4 + 1.390 (25.5 - ADF)
	graminoids	56.7	
	lichens	62.0	
winter	deciduous shrubs	36.0	48.6 + 1.090 (41.3 - ADF)
	evergreen shrubs	34.0	47.2 + 0.533 (28.2 - ADF)
	forbs	27.9	
	graminoids	44.7	
	lichens	62.0	

intermediate (1b) bogs. In upland habitats two representative sites of each type were selected and visits were alternated between the two. Five profiles constituted a visit. In 1985-86, profiles were performed at a single representative site, at or within 10 m of the aforementioned harvest macroplots. More emphasis was placed on bog habitats and the number of profiles per visit was reduced to four. In addition, jackpine forest (2) was a sandplain in 1985-86, and in 1984-85, an outcrop. Two days were required to sample each habitat.

At each profile, total thickness (cm), vertical hardness ($g \cdot cm^{-2}$), as well as the thickness and hardness of each layer were measured. These data represent the essential effects of api on Rangifer, and can be incorporated into a single measure, the Värriö Snow Index (VSI) (Pruitt 1979, 1981):

$$VSI = (H_{>1/2} \times H_b \times T_b + H_v \times T_s + H_h \times T_h) \times T_t / 1000$$

where $H_{>1/2}$ = hardness of the hardest layer more than half way up in the profile
H_b = hardness of the basal layer
T_b = thickness of the basal layer
H_v = vertical hardness
T_s = thickness of the surface layer
H_h = hardness of the hardest layer
T_h = thickness of the hardest layer
T_t = total thickness

If the basal layer is hardest then H_h and $T_h = 0$.

A repeated-measures design analysis of variance was used to test for habitat / age differences in log VSI. The

Ryan-Einot-Gabriel-Welsch multiple F-test (SAS 1982) was used to reveal means differences.

3.4.2 Windfallen Trees

During the summer of 1985, sampling was initiated to assess the effect of deadfalls as a barrier to caribou movements. This aspect of the project stemmed from the observation, while tracking animals during winter 1984-85, that caribou crossing burnt outcrops avoided areas dense with fallen trees.

Transects established during the vegetation survey during June and July 1985 were used to estimate the frequency of deadfalls in burned (both 5- and 9-year old) and mature stands. Along each transect (either 50 m north / south, or 25 m east / west) the number of downed trees (> 2.5 m upright) intersected was recorded. In all 271 transects (208 E/W and 63 N/S) extending over 8300 m were analysed.

During autumn of 1985 a more comprehensive sampling procedure was employed. Because pre-fire canopy was expected to influence the density of fallen timber, between-fire interval was recognised: sampling was partitioned between mature stands (burned in 1895, generally), 5.5 year burn (burned in 1895, 1980), 5.5 year burn (1929, 1980), and 9.5 year burn (1895, 1976). Sampling was restricted to an accessible area, identical to that used for the extensive vegetation survey, except that the areas surrounding Cabin Lake (5 km east of Wallace Lake) and Fox Lake were sampled in place of Obukowin Lake.

Discrete areas were chosen randomly, then 1:15,840 aerial photos and a grid overlay with dots interspaced by 200 m were used to select a point at random. This point was the origin of two transects: one in an east / west orientation, the other north / south. The length of each transect was determined with a spool of commercial thread, averaging 218.7 m ± 3.4 m (one standard deviation) in length (n = 6 spools). This average was treated as a constant for calculation of deadfall frequency per metre.

The number of downed trees intersected by the transect was tallied. In addition, the degree of stacking of trees was determined by classifying the height of the upper side of each bole to the nearest 0.5 m; this was accomplished with a graduated 2.5 m pole. In total, 63 transects covering over 7400 m were completed.

3.5 Habitat Utilisation:

3.5.1 Caribou Aerial Surveys

Survey flights during periods of snowcover were used to monitor caribou activity and facilitate more intensive ground reconnaisance. Surveys were flown approximately biweekly and required about 3 hours to complete.

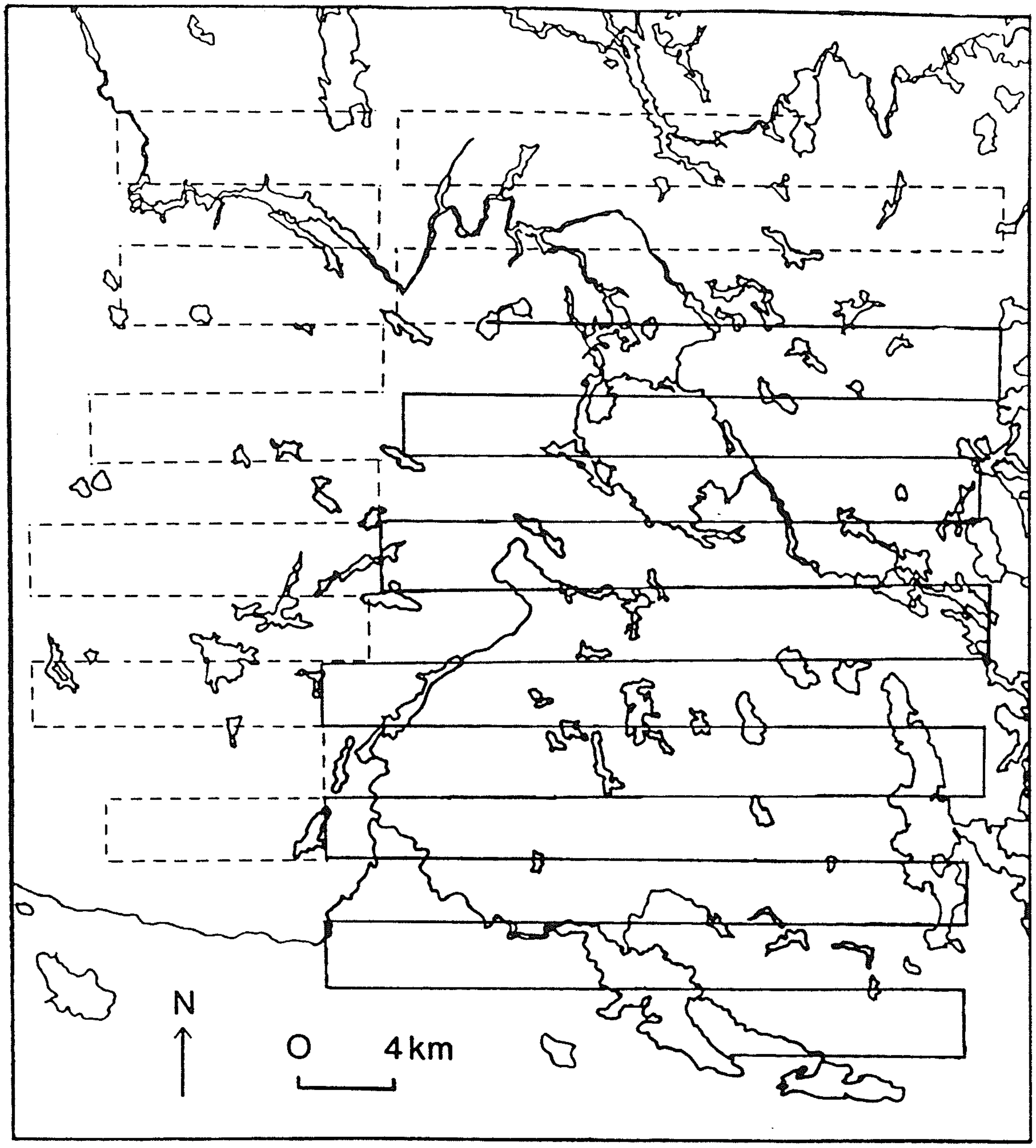
Procedure was modified from Darby (1979). A Cessna L-19, flown at 150 km $\cdot$ h^{-1} and 125 m altitude, followed twelve east west transects interspaced by 2.5 km (Figure 7). Two or three observers scanned a 0.2 km strip on either side of the aircraft, but in burned areas this strip was extend to 0.8 km to take advantage of greater visibility. The survey was extended north of Aikens Lake in February 1986; as well, additional western transects were flown on two supplementary surveys during March 1986 in response to the expansion of Aikens caribou range.

During flights, tracks, cratering, and sightings of caribou, moose (Alces alces andersoni), and wolves (Canis lupus lycaon) were recorded on a 1:56,000 photomosaic or 1:50,000 maps. Observations were translated into UTM grid reference numbers. Caribou were photographed with 35 mm film when sighted.

Caribou sign was distinguished from that of moose by the presence of cratering, extensive travel in bogs in single file, feeding on arboreal lichens, and groupings of seven or more animals. (Darby's [1979] criterion of a minimum four animals may be inadequate in itself since up to 6 moose were seen in close proximity during early winter.) Often, sign was simply noted as unidentified cervid.

A total of 14 flights were carried out over the two winters.

Figure 7. Flight lines for caribou aerial surveys. Dashed lines represent transects flown during extended surveys during 1986.


N
0
4km

Results were correlated with two range evaluation measures, log VSI and deadfall frequency. Caribou were classified on each flight as 'present' or 'absent' from burned and unburned uplands; animals were considered present, even if not observed during aerial surveys, if tracking could confirm use during the same biweekly api period. Mean log VSI, weighted by upland habitat type, and mean log deadfall frequency [(number $\cdot$ metre^{-1}) + 1] were used as habitat measures. These data were subjected to a multivariate F-test (Morrison 1976) to test for differences between the two groups. Canonical discriminant analysis (SAS 1982) was employed to derive a discriminant function, an 'api-deadfall index'.

3.5.2 Ground Searches and Tracking

Intensive on-ground investigations, primarily on skis, were conducted to search for caribou and their sign during periods of snowcover. Most searches were confined to the limits of the study area vegetation map. Occasionally, outcamps were established to extend the area surveyed, but investigations were most intense in the area bounded by Aikens, Leaf, and Fox lakes and Highway 304. Trails tended to follow semi-open and intermediate bogs, lakes, and rivers.

Once sign was encountered, tracking usually proceeded in the 'forward' direction; if animals were sighted, backtracking was used to avoid disturbance. Point of intersection, estimated date of occurrence, location of pellet groups, location and type of feeding sites, and direction and route of travel were first recorded on 1:15,840 aerial photos, then transcribed onto the vegetation map. Group size was determined when caribou fanned out on lakes or rivers, but in some instances these estimates represent minima. Tracking of a single group normally lasted one or two days and ranged from 1 to 10 km. Obliteration of tracks by fresh snow often hampered survey efforts.

The number of 'caribou · kilometres' of travel was used as an index of the relative utilisation of study area habitats. This index was simply the product of group size by the distance travelled (to the nearest 0.1 km), determined using a map measurer. Discrete pellet groups and feeding sites were additional use indices. A single crater (suov'dnji) or tree exploited for arboreal lichens constituted one feeding observation. Although samples are not independent, a chi-square analysis (Steel and Torrie 1980) using 1 degree of freedom was used to reveal preference or avoidance of study area habitats.

While tracking animals during 1985-86, deadfall intersection rate was recorded on 3 occasions. Tallying procedure followed that for random transects (Windfallen

Trees, Section 3.4.2). In addition, two staight-line transects were analysed over burned ridges that animals had circumvented. These data, in conjunction with mean log VSI (weighted by upland habitat composition), were used to test the 'api-deadfall index' employing the SAS discriminant procedure (SAS 1982).

4. RESULTS

4.1 Ordination of Plant Communities

The effectiveness of principal components analysis (PCA) in revealing relationships between plant communities lies in its ability to reduce the number of dimensions needed to display a data set, while retaining much of its original information (Pielou 1984). PCA was applied to data from Wallace Lake plant communities to test the efficacy of the habitat stratification (both in its original state and after burning) and to ensure that harvest sites were representative.

Displays of the first and second principal components are presented for mature, intermediate, and burned upland plant communities in Figures 8, 9, and 10 respectively. An earlier PCA of all sites from all ages (not presented) simply separated the age classes and thus failed to reveal between-community structure. Thus separate analyses were performed by age class.

In all cases the first two principal components accounted for 28 to 43 % of the variance. Higher order axes did not appear to improve habitat separation. Although PCA axes are not necessarily ecologically independent or even interpretable (Austin 1985), the first component is similar in all three cases and is related to moisture availability.

Figure 8. Plot of first and second principal components for mature upland sites. Numbers represent habitat types (2 represents sandplains rather than outcrops). Circled individuals were chosen as harvest sites. Axis labels in parentheses indicate the respective proportions of the total variance explained.

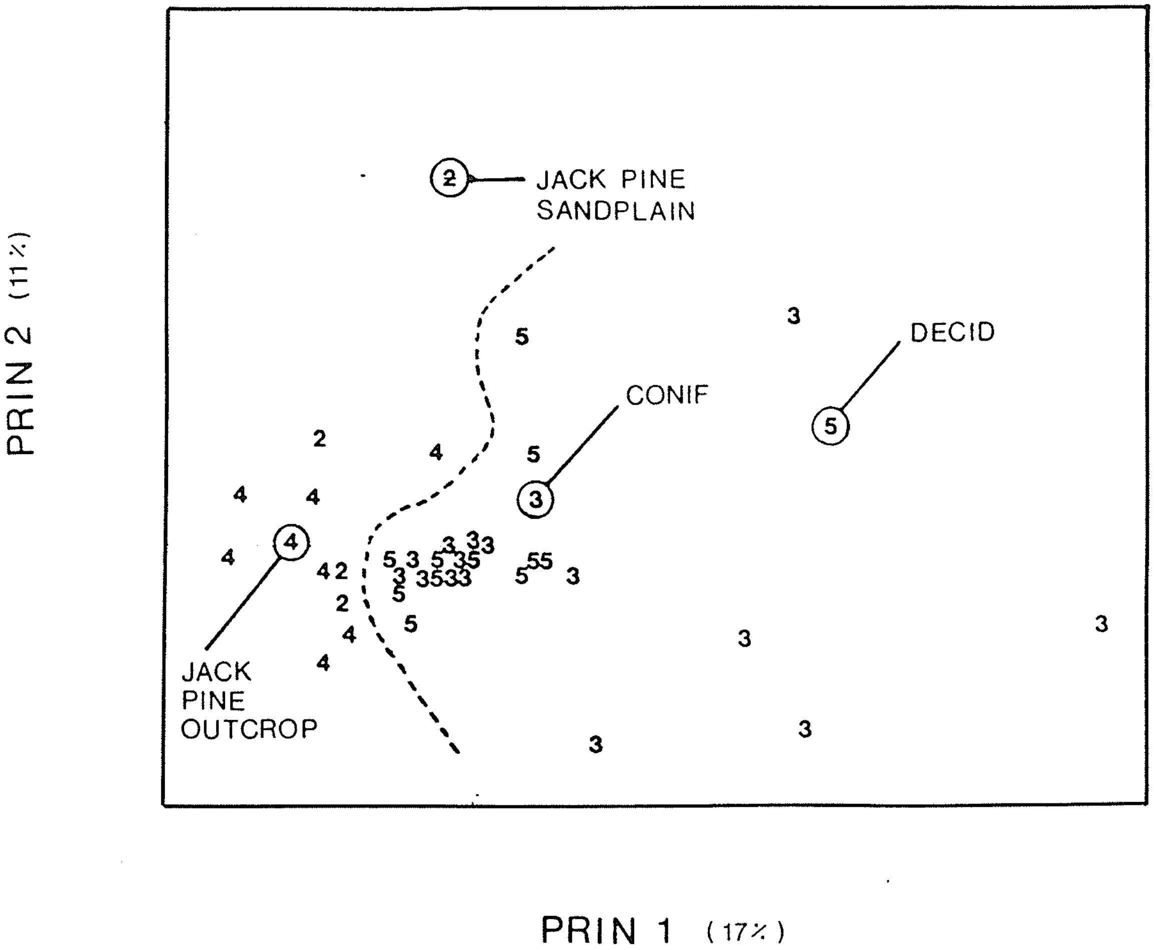

JACK PINE SANDPLAIN
DECID
CONIF
JACK PINE OUTCROP
PRIN 2 (11%)
PRIN 1 (17%)
2
3
4
5

Figure 9. Plot of first and second principal components for intermediate upland sites. Numbers represent habitat types (2 represents sandplains rather than outcrops). Circled individuals were chosen as harvest sites. Axis labels in parentheses indicate the respective proportions of the total variance explained.

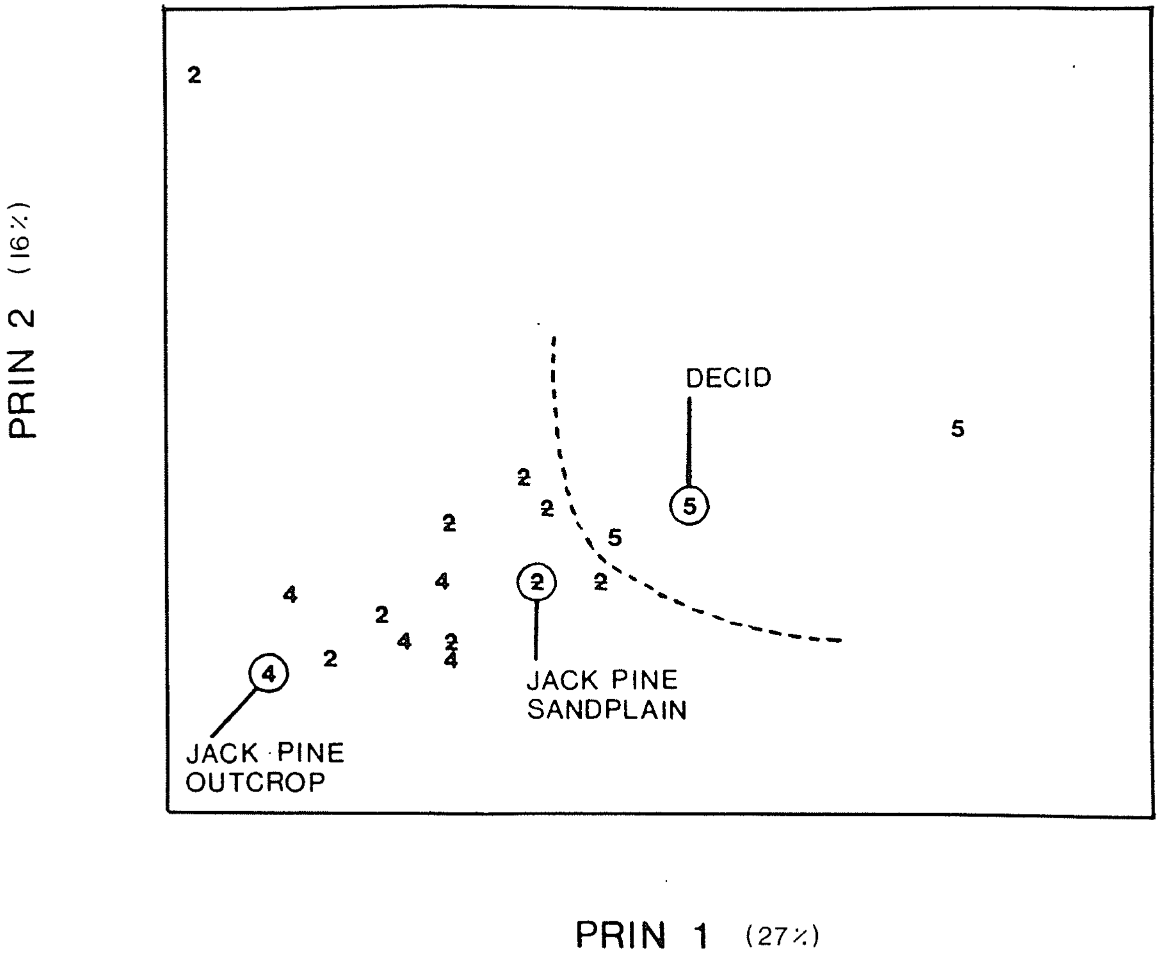
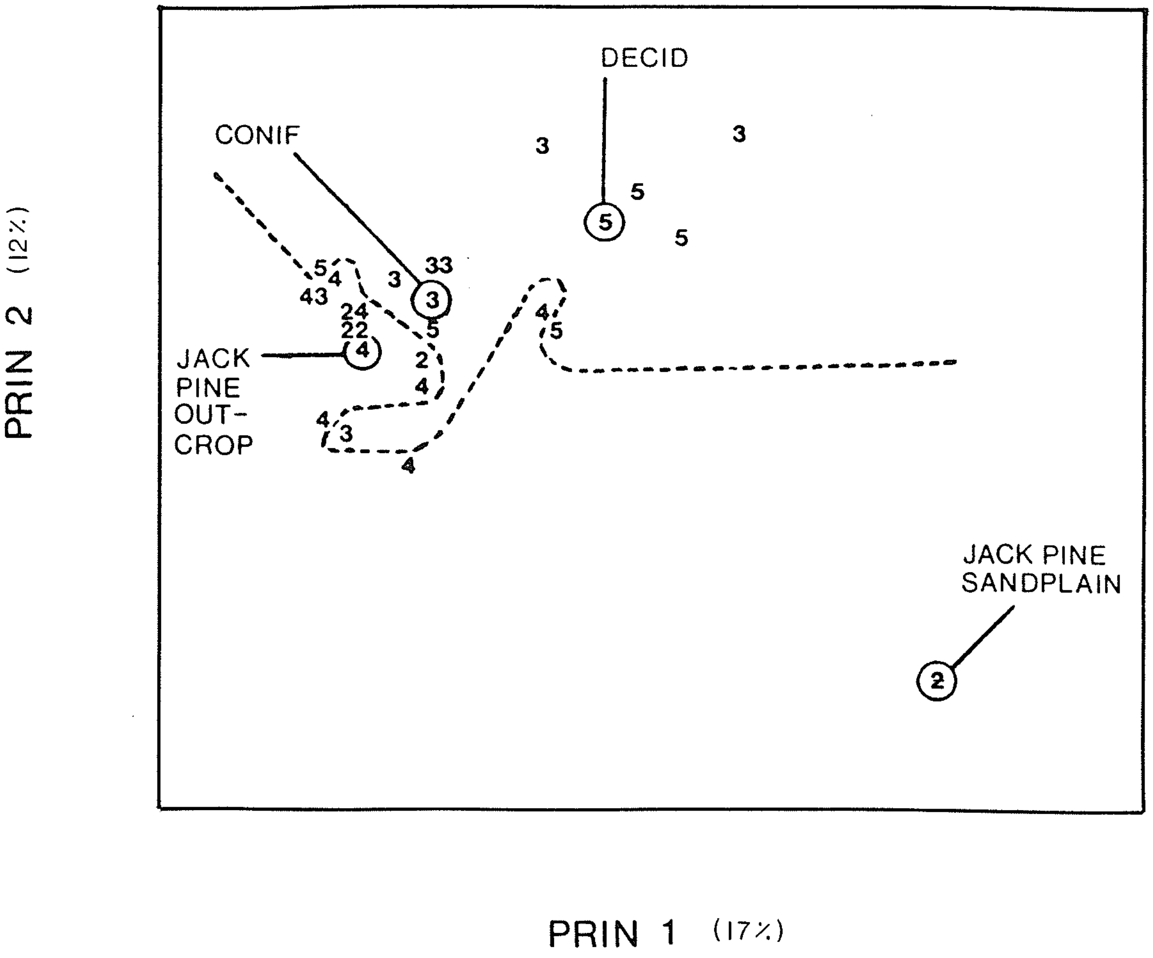

PRIN 2 (16%)
PRIN 1 (27%)
DECID
JACK PINE SANDPLAIN
JACK PINE OUTCROP
2
5
2
2
2
5
4
4
2
2
2
4
2
4
2
4
5
2
4

Figure 10. Plot of first and second principal components for burned upland sites. Numbers represent habitat types (2 represents sandplains rather than outcrops). Circled individuals were chosen as harvest sites. Axis labels in parentheses indicate the respective proportions of the total variance explained.


DECID
CONIF
3
3
33
3
5
5
5
5
54
43
3
24
22
4
JACK PINE OUT-CROP
2
4
4
3
4
4
5
JACK PINE SANDPLAIN
2
PRIN 1 (17%)
PRIN 2 (12%)

The second dimension for burnt habitats is also moisture-related, but seems to reflect the abundance of mesic shrubs (Populus, Ribes, and Rubus idaeus) over more xeric species (Arctostaphylos uva-ursi, Vaccinium species). For intermediate habitats the second component tends to separate outcrops from closed-canopy sites. The second axis for mature habitats appears sensitive to the interspersion of boggy sites: Sphagnum, Ledum, and Gaultheria hispidula have high negative eigenvectors, while species characteristic of more uniformly xeric sites (Chimaphila umbellata, A. uva-ursi, and Vaccinium species) are highly positive.

Although the original stratification recognises four distinct upland habitats, this community separation was not borne out in the ordination results; rather, Wallace Lake plant communities are distributed continuously. Furthermore, not only are jack pine habitats 2 (when on outcrop) and 4 essentially indistinguishable (as suggested by the original classification), but no obvious separation between habitats 3 and 5 can be discerned. There is however, a strong distinction between jack pine and mixed forests; this disjunction is most complete in mature condition, but becomes somewhat obscured after burning.

This loss of community distinction following fire appears attributable to the invasion of successional species (Epilobium angustifolium, Polygonum cilinode, Rubus ideaus, legumes, and graminoids), common to almost all burned habitats. Community segregation may tend to progress with time; after several years, with the onset of canopy closure and the elimination of early successional plants, sites may achieve greater floristic divergence, as is the case for intermediate-aged habitats.

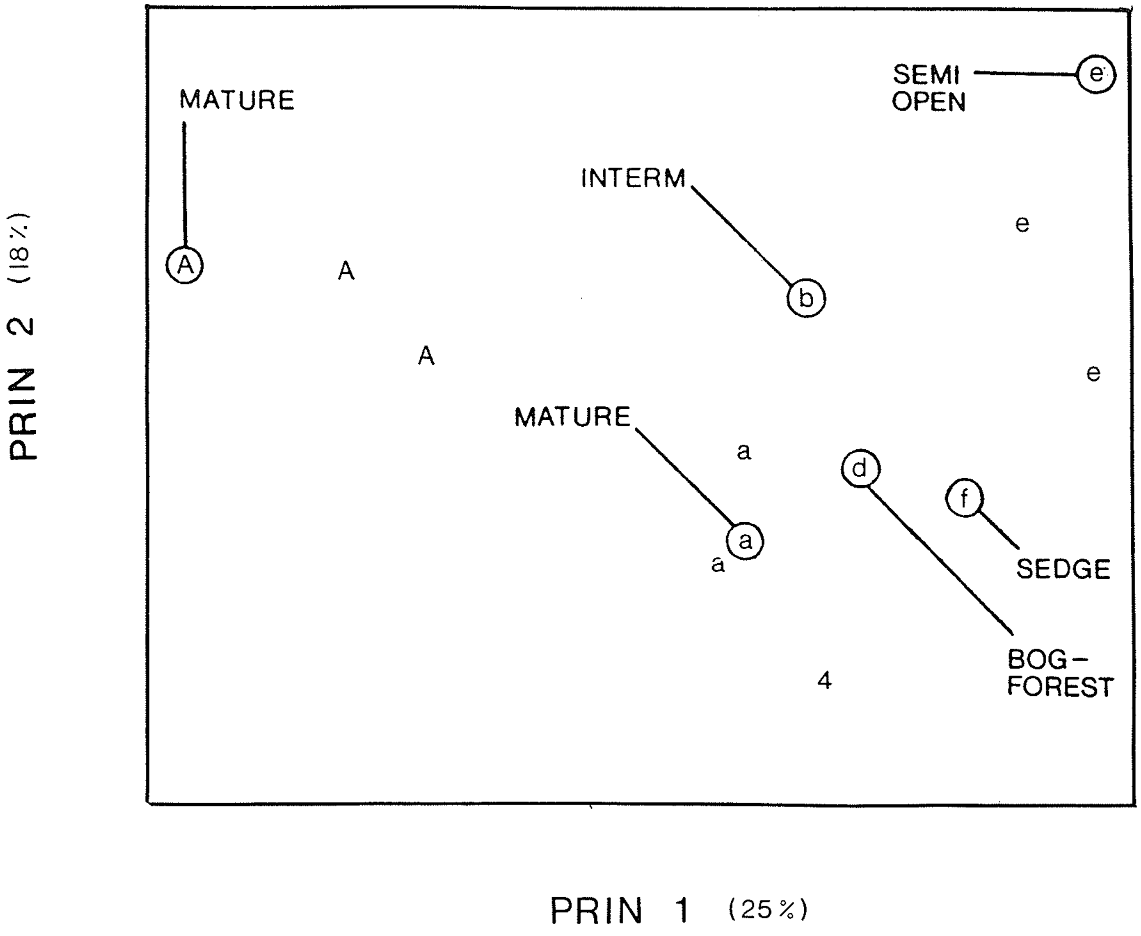
Sites selected for productivity estimates are, in most instances, satisfactory representatives of their community types. Mature site 5 appears to overestimate the abundance of several species (*Diervilla lonicera*, *Cornus canadensis*, *Ledum groenlandicum*, *Lycopodium annotinum*), resulting in a somewhat extreme position on both axes. As well, intermediate site 4 may overestimate the abundance of *Cladina* species. Finally, jack pine sandplain representatives (2) are outliers in the mature and burned cases, but this was not unexpected. For the purposes of this study, habitat 2 was further partitioned into sandplains and outcrops; because sandplains constitute only a small fraction of the study area (Table 1), all randomly-located sites from habitat 2 during the vegetation survey happened to be over outcrops rather than sand. The representativeness of this harvest site thus requires verification. Notice, however, that the typical intermediate jack pine sandplain is well-placed among several examples of habitat 2; these five sites closest on axis 1 were found to have a sandy substrate at least in part.

Note as well an outlier of intermediate habitat 2 (Figure 9). This site contained most plant species which had high loadings -- *Arctostaphylos uva-ursi*, *Cladina* species, *Potentilla tridentata* had highly negative values on the first axis, while *Maianthemum canadense* and *Diervilla lonicera* were highly positive on the second -- and hence is a somewhat spurious result.

Finally, the PCA of bog communities also revealed that typical harvest sites were representative, although perhaps extreme in the case of 1e bogs and burnt 1a types (Figure 11). In the former, the high score on the second axis seems to stem from the higher densities of ericaceous shrubs and the absence of *Salix* compared to the two random sites. In the latter, the low score on the first axis results from the higher abundance of *Ledum groenlandicum* and *Vacciinium vitis-idaea*.

For these bog sites, overall, the two axes account for 43 % of the variance, and relate to overall moisture availability (axis 1) and to the abundance of evergreen shrubs over deciduous types (axis 2). Note that the lone example of an intervening black spruce bog from habitat 4 is most closely approximated by data from the mature (1a) bog site.

Figure 11. Plot of first and second principal components for bog sites. Letters represent habitat subtypes; those in capitals are burned. Circled individuals were chosen as harvest sites. Axis labels in parentheses indicate the respective proportions of the total variance explained.

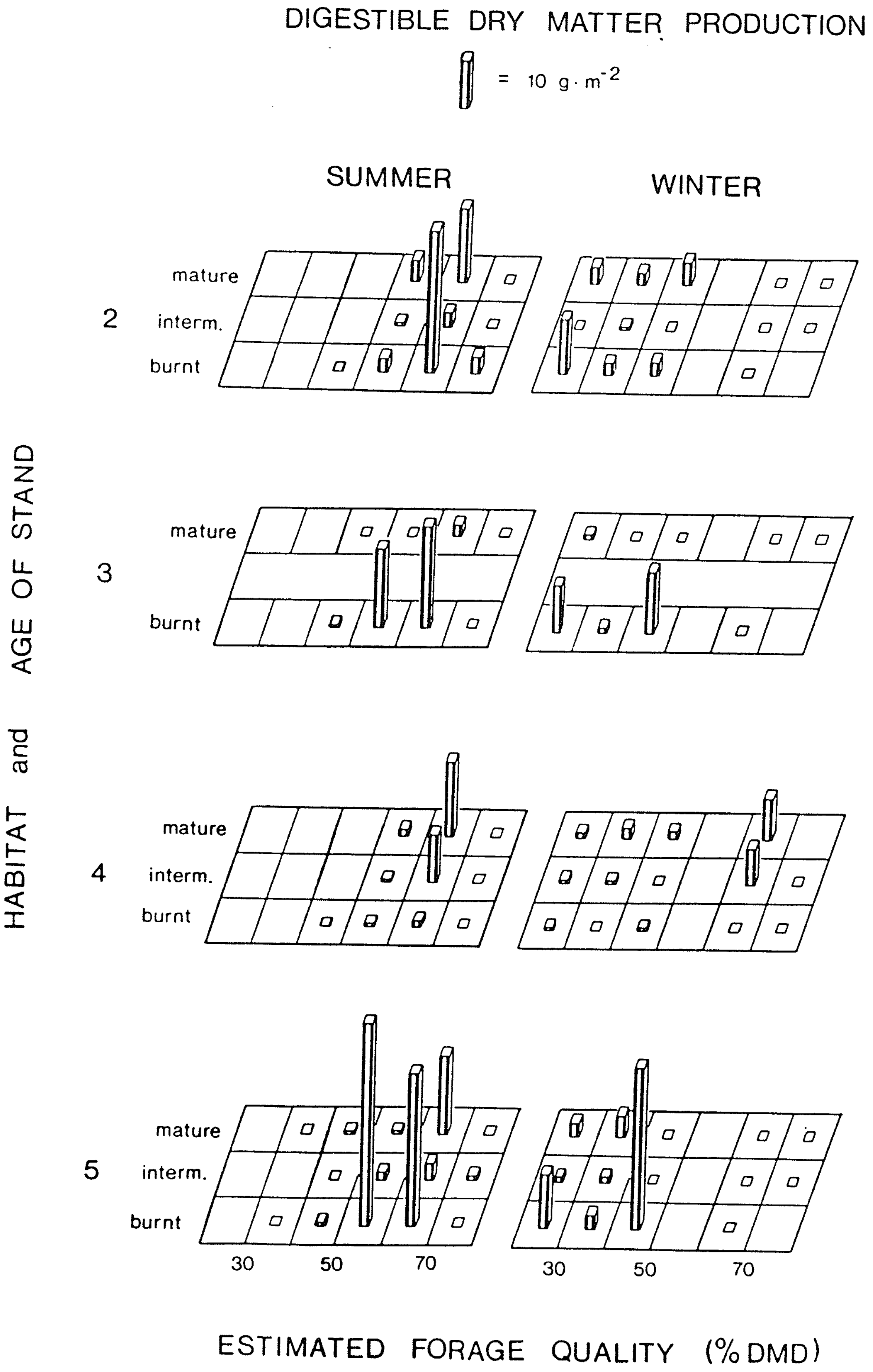

MATURE
SEMI OPEN
INTERM
MATURE
SEDGE
BOG-FOREST
A
A
A
a
a
a
b
d
e
e
e
f
4
PRIN 2 (18%)
PRIN 1 (25%)

4.2 Forage Productivity

Fire in the Wallace-Aikens area has a profound effect on the productivity of digestible dry matter and its distribution. Supplies of DDM are the result of interactions of habitat type, time of year, and time since burning.

The relative yield of summer forage for upland communities is presented in Figure 12. Plant species were placed into one of six digestibility classes to clarify the distribution of food quality. Because the value of forages is generally high (> 50% digestible) for summer habitats, differences can largely be ascribed to forage abundance. It is clear that most communities produce copious quantities of forage. This is especially evident for burned habitats when forbs (Epilobium angustifolium, Cornus canadensis, Equisetum sylvaticum) and deciduous shrubs (Populus species, Rubus idaeus, Vaccinium species) are plentiful. There is a dramatic decline for stands of intermediate age --the mean is as low as 2.6 g DDM . m^{-2} for sandplains -- then a recovery to varying degrees once 'maturity' is reached. Note, however, that the Figure 12 does not imply a direct successional sequence. It is noteworthy that mature sites 3 and 5 were found to be of greater age (about 160 years) than jackpine habitats (90 years).

Figure 12. Quantity and quality of caribou forages for upland habitats (2= jack pine sandplain, 3= mixed coniferous forest, 4= jack pine outcrop, 5 = mixed deciduous forest) by season and age of stand (burnt= 5 years, intermediate = 37 years, mature = 90+ years). Height of bar represents productivity of digestible dry matter. Forages are partitioned by classes of dry matter digestibility (DMD).



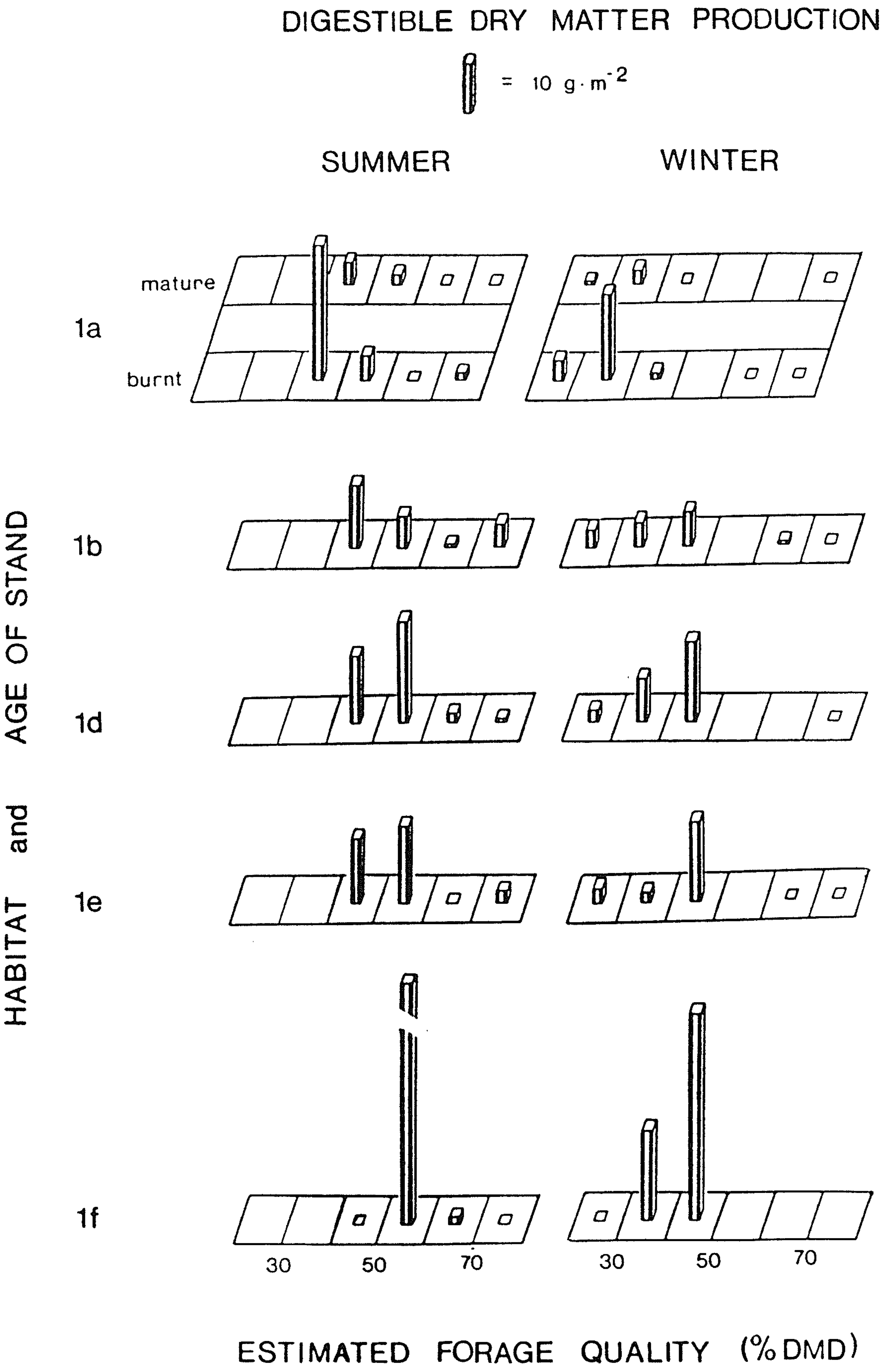
DIGESTIBLE DRY MATTER PRODUCTION

Significantly, jackpine outcrop communities (4) deviate from this trend. The loss of forage resources immediately after burning is substantial, largely due to the combustion of Cladina lichens. However, the vegetation aerial survey indicated that 7.0 km^2 of lichen outcrop had survived the 1980 fire; these 'crowned-off' areas occurred almost exclusively in the stands originating in 1929, to the west of Fox Lake. In any case, post-fire recovery appears linear with time; maximal resources are attained in the mature condition for habitat 4.

Winter, too, affects upland habitats differentially. A decline in forage quality is universal, but is most pronounced for forbs and consequently for burned communities. Quality on jack pine ridges is less susceptible to this seasonal change, again due to the high lichen component.

Bog habitats are characterised by their high productivity of relatively low quality summer forage (Figure 13). An average of up to 83.9 g DDM $\cdot$ m^{-2} may be found in sedge (1f) meadows. Bog forages appear to be less sensitive to the onset of winter, primarily due to the preponderance of shrubs (Kalmia polifolia, Chamaedaphne calyculata, Salix species) and graminoids over forbs. Arboreal lichen estimates (Appendix C) are included here for intermediate (1b) and semi-open (1e) bogs; their contribution (x = 0.75 and 0.31 g dry matter . m^{-2}, respectively) appears minor

Figure 13. Quantity and quality of caribou forages for bog habitats (1a= mature bog, 1b= intermediate bog, 1d= bog-forest, 1e= semi-open bog, 1f= sedge meadow) by season and age of stand (burnt = 5 years, mature = 90+ years). Height of bar represents productivity of digestible dry matter. Forages are partitioned by classes of dry matter digestibility (DMD). Habitats were unburned unless otherwise indicated.



DIGESTIBLE DRY MATTER PRODUCTION
= 10 g·m⁻²
SUMMER
WINTER
mature
burnt
1a
1b
1d
1e
1f
HABITAT and AGE OF STAND
30
50
70
30
50
70
ESTIMATED FORAGE QUALITY (%DMD)

compared to total vascular plant production, however. Finally, burning of the most susceptible bogs (mature 1a) enhances overall forage yield -- *Ledum groenlandicum* and *V. vitis-idaea* are plentiful -- but, similar to most uplands, there is only a marginal increase in the quality of forages.

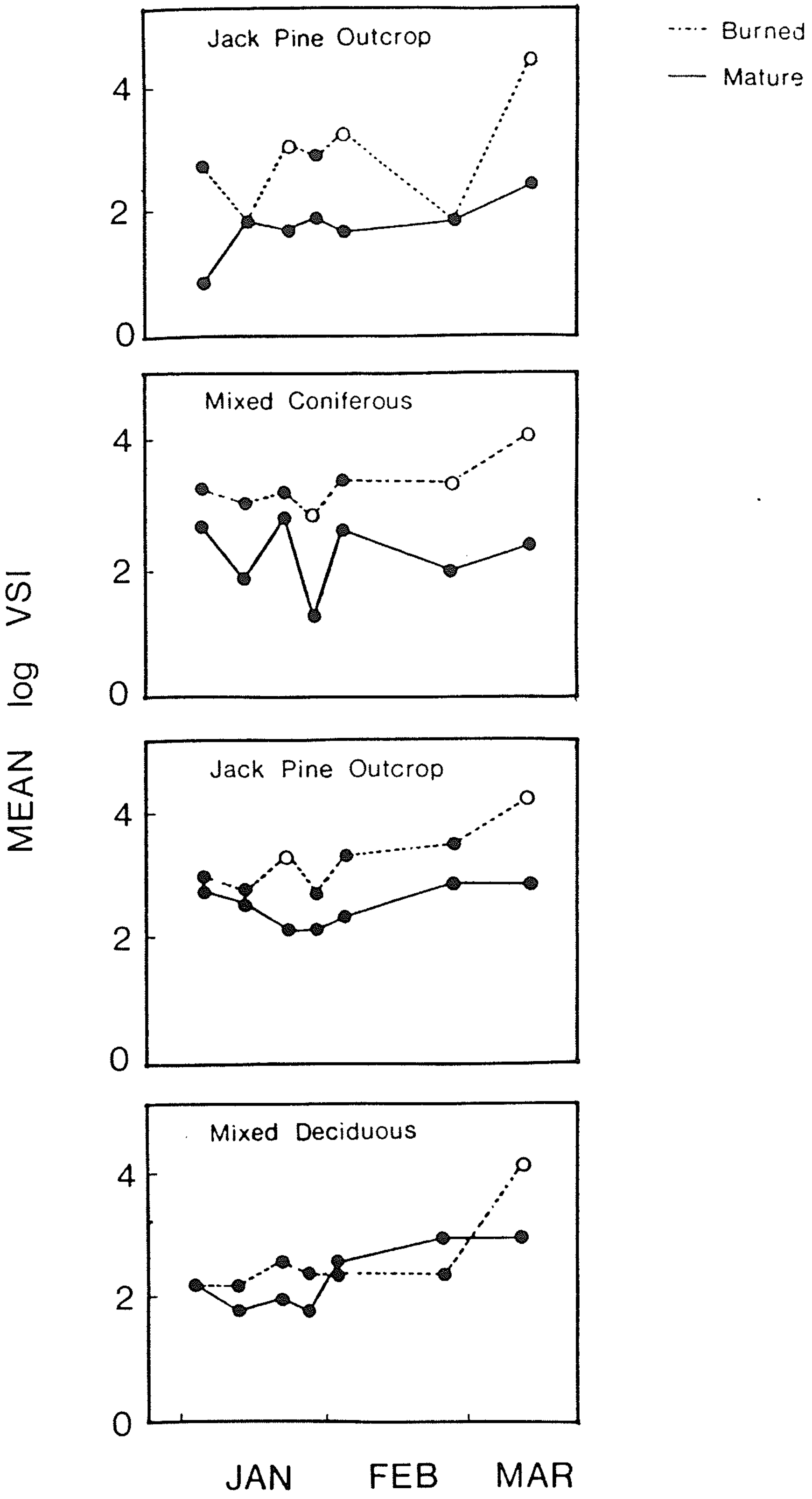
4.3 Api Conditions

In general, burning of taiga habitats adversely affected api (snow) conditions for Aikens caribou: mean log VSI was substantially elevated for burned habitats compared to their mature analogues ($F_{1,32} = 177$, 1984-85; $F_{1,30} = 303$, 1985-86; $p < 0.001$ for both winters) (Figures 14 and 15).

This trend, however, is not simply a function of time since burning. Habitats responded differently to burning (habitat-age interaction, $F_{3,32} = 12.8$, 1984-85; $F_{4,30} = 27.3$, 1985-86; $p < 0.001$, both winters): those with more closed canopies (habitats 1a, 3, 5) generally were more greatly affected, while jackpine communities showed variable results from the two winters. Yet by late winter, the difference between burned and mature habitats was expressed in virtually all community types.

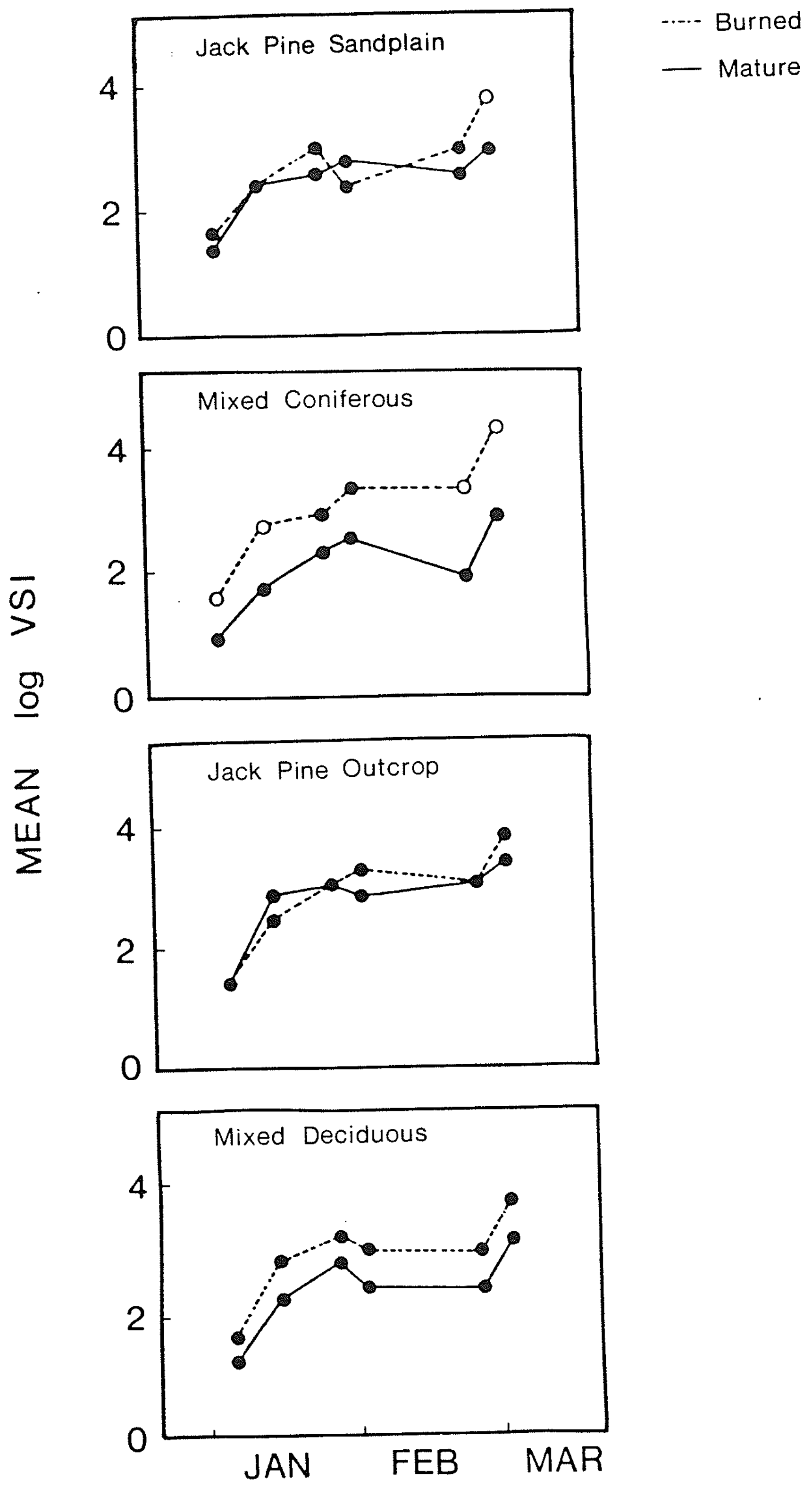
Which components of VSI are responsible for this discrepancy? Aggravated snow conditions apparently were attributable to increased total thickness in burned-over sites for most of the season. By late winter the difference in VSI was accentuated by increased vertical hardness in burned areas; apparently the lack of shade allowed formation of a harder sun crust, and more severe thaw-freeze conditions.

Figure 14. Mean log VSI for upland habitats during 1984-85 in burned and unburned condition. Open circles represent significant differences ($p < 0.05$) between analogues.



Burned
Mature
Jack Pine Outcrop
Mixed Coniferous
Jack Pine Outcrop
Mixed Deciduous
MEAN log VSI
0
2
4
JAN
FEB
MAR

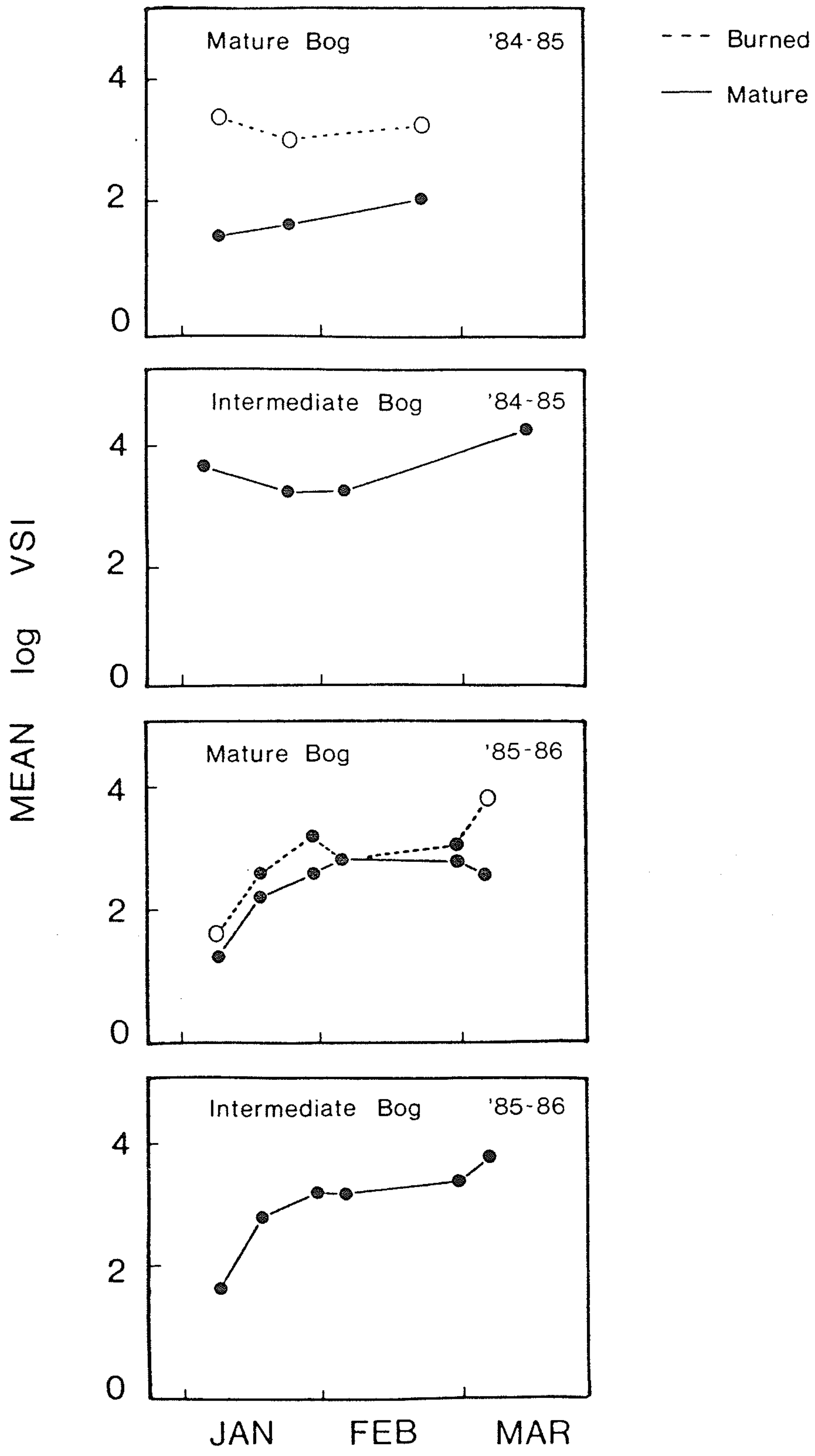
Figure 15. Mean log VSI for upland habitats during 1985-86 in burned and unburned condition. Open circles represent significant differences ($p < 0.05$) between analogues.


Burned
Mature
Jack Pine Sandplain
Mixed Coniferous
Jack Pine Outcrop
Mixed Deciduous
MEAN log VSI
0
2
4
JAN
FEB
MAR

Interestingly, the years differed in the magnitude of the difference between the two age classes. In 1984-85, snowfall and temperatures were about normal. A thaw and refreeze in November created a hard basal layer (circa 500 g $\cdot$ cm^{-2}) which persisted in most profiles for the winter's duration, but did not affect VSI greatly. The next winter was considerably milder. On 11 January 1986, in particular, a high of 7.5 ^{o}C was combined with 4.6 mm of rain; the low temperatures on the next two days (-19 ^{o}C and -20 ^{o}C) resulted in a substantial rise in VSI. Its differential effect on burned and unburned habitats, however, was less severe than that of total api accumulation or the development of a late-season ice crust.

Bog habitats, as exemplified by intermediate (1b) bogs, were typified by harder and thicker snowcover than that in upland types. Their mean VSI values are correspondingly elevated (Figure 16). Through most of the season the difference is due to thicker api, and in late winter, harder api. Compared to uplands, significant ($p < 0.05$) differences exist only with mature closed-canopy habitats (particularly habitat 3) during early and mid-season, but by late winter nearly all unburned uplands have significantly lower VSI values. This lowland-upland discrepancy is essentially eliminated once uplands are burned, however.

Figure 16. Mean log VSI for bog habitats during 1984-85 and 1985-86 in burned and unburned condition. Open circles represent significant differences ($p < 0.05$) between analogues.


Mature Bog
'84-85
Intermediate Bog
'84-85
Mature Bog
'85-86
Intermediate Bog
'85-86
MEAN log VSI
0
2
4
JAN
FEB
MAR
- - - Burned
—— Mature

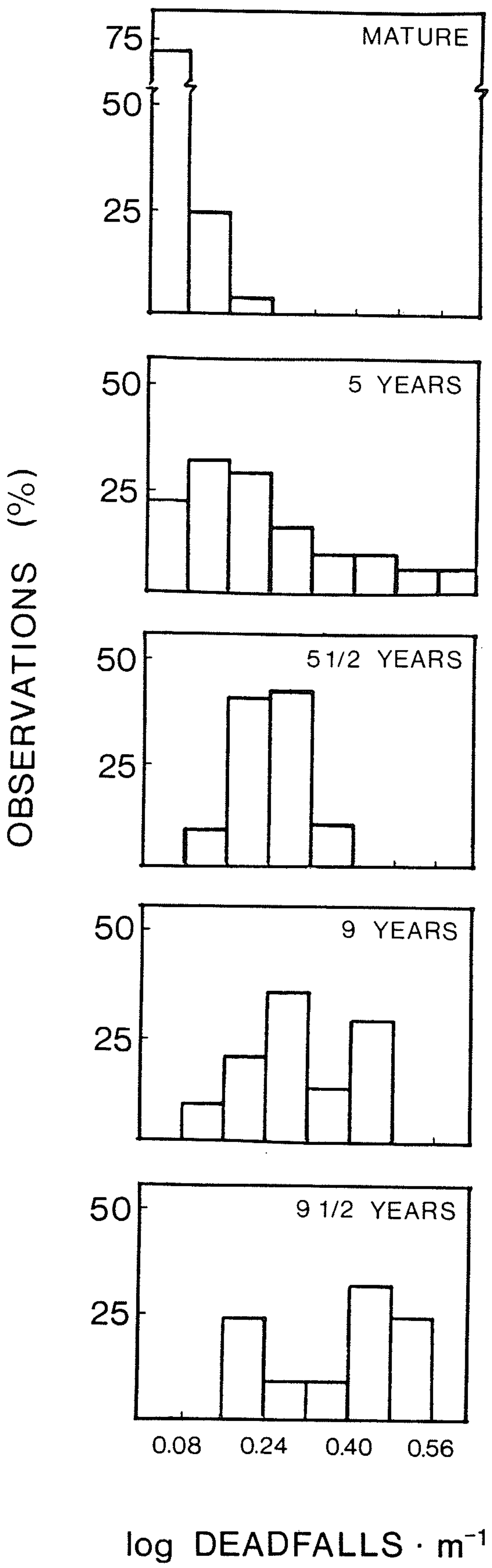
4.4 Windfallen Trees

The occurrence of deadfalls for taiga habitats is highly dependent on time since burning ($F_{5,324} = 64.6$, $p < 0.0001$). Significant differences exist between the log frequency of all age classes ($p < 0.05$, Tukey HSD = 0.77) except for mature areas between the two sampling periods, and between stands of 5 years and 5.5 years; this latter comparison was substantial (difference = 0.48) if not statistically significant.

By 5.5 years, burned stands exhibit dramatic increases in total deadfall abundance (mean = 0.78 trees . m^{-1}). Data from the summer vegetation survey indicate that this rate corresponds to approximately 49 % of trees downed (688 of 1415 trees), but densities can attain 1.39 trees . m^{-1}. For the 9.5 year old burn, where about 90 % of the trees have fallen (255 of 266), the average exceeds 1.5 trees . m^{-1} and may reach more than 2.5 trees . m^{-1}. Unburned areas, for comparison, average only 0.16 trees $\cdot$ m^{-1}. This progression with time is illustrated in Figure 17.

Up to 5.5 years, no habitat difference could be discerned when one-way ANOVAs were performed on mixed versus jackpine habitats ($p > 0.10$, all tests). A difference was expressed, however, by 9.5 since burning: jackpine communities showed greater densities than did mixed types ($F_{2,11} = 754$, $p < 0.0001$).

Figure 17. Distribution of log deadfall frequency (number $\cdot$ m^{-1} + 1) for upland sites at various ages.


MATURE
75
50
25
5 YEARS
50
25
5 1/2 YEARS
50
25
9 YEARS
50
25
9 1/2 YEARS
50
25
0.08
0.24
0.40
0.56
OBSERVATIONS (%)
log DEADFALLS · m⁻¹

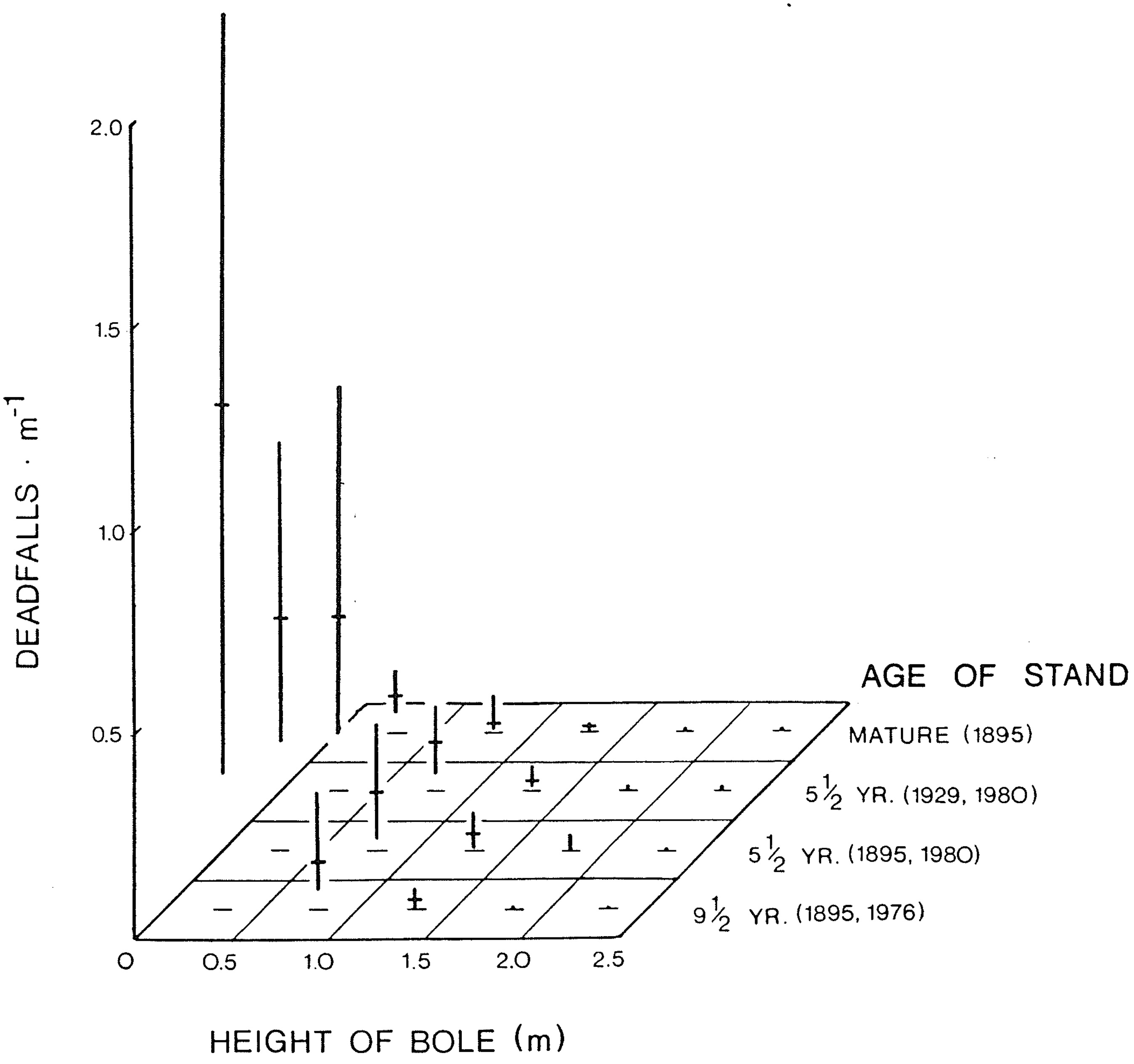
Orientation of transects did not affect intersection rate; data from autumn 1985 for the 5.5 year old burn indicated no difference between north / south versus east / west transects (n = 33, Wilcoxan paired W+ statistic = 0, $p > 0.30$).

The more detailed analysis during autumn 1985 permits comparisons of deadfall frequency at various stacking heights. Figure 18 reveals that differences related to time since burning are largely due to the accumulation of downed boles at less than 0.5 m above the ground. Note that above this 0.5 m level all burned areas are essentially similar, but remain substantially different from mature stands (90+ years) at 0.5 m to 1.0 m. Boles at a stacking height of over 1.0 m make only a minor contribution to overall windfall frequency and are not remarkably dissimilar across ages. Finally, it appears that date of previous fire (1895 versus 1929) has no marked impact on deadfall density at any height, at least for stands of 5.5 years of age.

4.5 Habitat Utilisation

During 1984-85 (24 November to 10 March), 18 separate tracking events yielded identification of 361.3 caribou · km of travel, 554 feeding sites, and 207 pellet groups. Interception of caribou sign occurred most frequently west

Figure 18. Ranges and means (horizontal bars) of deadfall frequency (number · m^{-1}) for upland sites sampled during autumn 1985 in relation to stand condition and stacking height of bole. Numbers in parentheses represent year of occurrence of fires for the stands.


DEADFALLS · m^{-1}
2.0
1.5
1.0
0.5
0
0.5
1.0
1.5
2.0
2.5
HEIGHT OF BOLE (m)
AGE OF STAND
MATURE (1895)
5½ YR. (1929, 1980)
5½ YR. (1895, 1980)
9½ YR. (1895, 1976)

of Wallace Lake and south and west of Fox Lake. Aikens caribou frequently traversed burned outcrops, and made heavy use of lakes and bogs (particularly 1b, 1e, and 1f types). Table 5 presents the relative use of study area habitats indicated by travel, feeding, and pellet locations, in relation to habitat availability. Habitats 2 and 4 (jack pine forests) and 3 and 5 (mixed forests) are combined, as suggested by the ordination results, in order to simplify analysis.

Although caribou often made use of burned uplands, almost all measures of use indicate avoidance of these habitats. Conversely, most bog communities, lakes, and roads were exploited more frequently than their occurrence. Significantly, travel in 1985-86 indicated a selection for unburned jack pine habitats (2 and 4), whereas this selection was absent the previous winter.

Similarly, feeding sites are skewed in favour of more-open bogs and jack pine habitats; crown-burned outcrops (with intact lichens) accounted for almost all foraging in burned communities (Figure 19).

Cladina lichens were the item exploited overwhelmingly at caribou feeding sites, particularly at intact 'islands' of jack pine forest in bogs and at crowned-off jack pine ridges (Table 6). Additionally, arboreal lichens (Usnea hirta, Bryoria trichodes, Evernia mesomorpha), foliose lichens along lakeshores (Umbilicaria species), sedges, and

Table 5. Availability and winter utilisation of habitats by caribou for 1984-85 and 1985-86. Preference (+) and avoidance (@) of communities are indicated ($p < 0.01$). Categories with less than 0.5% are blank.

Age of Stand	Community Type[a]	Availability[b] (%)	Winter Utilisation (% of Obs.)			
			Travel[c] 1984-85	Travel[d] 1985-86	Feeding[e] 1984-85	Pellets[f] 1984-85
burned 1976 (8-9 yrs.)	1a					
	1b					
	1d					
	1e					
	2 & 4	2.5	0.0 @	0.0	0.0 @	0.0
	3 & 5	0.5	0.0	0.0	0.0	0.0
burned 1980 (4-5 yrs.)	1a	1.5	3.1	1.1	0.3	2.9
	1b	0.0	0.0	0.0	0.0	0.5
	1d	0.5	0.0	0.0	0.0	0.5
	1e					
	2 & 4	41.8	25.1 @	12.4 @	25.2 @	31.4
	3 & 5	11.5	2.7 @	1.2 @	0.0 @	0.5 @
unburned (50+ yrs.)	1a	2.5	2.3	9.2 +	0.6 @	4.3
	1b	9.0	10.1	28.9 +	6.3	8.7
	1d	1.0	3.0 +	0.0	0.0 @	0.0
	1e	7.0	11.1 +	8.3	11.2 +	6.2
	1f	0.5	7.9 +	0.0	2.4 +	3.4 +
	2 & 4	5.5	4.8	12.9 +	41.7 +	30.0 +
	3 & 5	3.0	0.0 @	0.0	0.0 @	0.0
	lakes	13.4	25.1 +	23.2 +	12.6	11.6
	roads		5.0 +	2.7 +		
Totals		100.0	100.0	100.0	100.0	100.0

[a] Habitat 4 bogs are represented by 1a bogs. Lakes include areas within 10m of shoreline.

[b] Based on photo-interpretation of 201 UTM grid points within the ground search area

[c] n = 361.3 caribou · km

[d] n = 96.5 caribou · km

[e] n = 554 feeding sites

[f] n = 207 pellet groups

Figure 19. Caribou feeding craters near Correction Lake, February 1985. Outcrop had suffered a crown-only fire in 1980, leaving the lichen substrate intact.

Table 6. Percent occurrence of plant species utilised at caribou feeding sites during winter 1984-85.

Species	Percent Occurrence at Feeding Sites (n = 554)
Cladina species	53.7
Usnea/Evernia/Bryoria	18.2
Umbilicaria species	14.8
graminoids	5.0
Kalmia polifolia	3.6
Cladonia species	3.6
Andromeda glaucophylla	2.5
Arctostaphylos uva-ursi	2.0
Chamaedaphne calyculata	1.6
Vaccinium species	1.4
Stereocaulon species	0.8
Vaccinium vitis-idaea	0.8
Gaultheria procumbens	0.3
Juniperus species	0.2
Epilobium angustifolium	0.2
Compositae	0.2

the leaves of ericaceous shrubs made significant contributions. Avoidance of Ledum groenlandicum, dried forbs, and woody material was nearly complete: only two instances of feeding on dried forbs, emerging above the api, were noted.

Documentation of seasonal progression of habitat use, although limited, is consistent with VSI measures. The final tracking event of winter 1984-85 (11.2 caribou · km on 17 March 1985) indicated no travel in any bog community, coincident with an increase in hardness and a sharp rise in log VSI to about 4.2; this was the only observation with such an absence of use. At this time, caribou travelled exclusively in upland habitats, and then moved to unburned (55-year old) stands.

Tracking effort during 1985-86 was severly hampered by the paucity of any caribou activity, particularly within the limits of recent burns and vegetation map. Only 2 intensive tracking events were documented, the latter on 9 December 1985. Ground reconnaissance was not re-established until 21 March 1986, when tracks of 3 animals were noted 2 km west of Aikens Lake. Although sample size is small (96.5 caribou · km) (Table 5), results illustrate that avoidance of burned uplands was more pronounced than the previous winter, with a corresponding and significant increase in travel in bogs and unburned jack pine habitats. Observed feeding behaviour was minimal, but in accordance with the previous year's data.

Winter aggregate ranges of Aikens caribou determined by aerial surveys are consistent with ground investigations. Significant dissimilarity exists between the population's pre-fire range, 1984-85 range, and 1985-86 range (Figure 20). Four and one-half years after fire, Aikens caribou continued to exploit habitats within the burn, including not only much of their original range but also west into 55 year old stands (Figure 21). Animals ceased to use burned habitats by 20 March 1985, when VSI in burned areas had increased dramatically over that in unburned areas.

By five and one-half years, caribou occupied a region mutually exclusive to their pre-fire range and essentially exterior to the limits of the 1980 fire (Figure 22). After December 1985, not a single instance of use of burned-over habitats was noted. Similarly, utilisation of communities within the 1976 burn was minimal in 1984-85, and absent in 1985-86. Note, furthermore, the expansion in size of winter range from Darby's (1979) estimates (Figure 20).

Figure 20. Pre-fire and post-fire winter ranges of Aikens caribou. Pre-1980 ranges adapted from Darby (1979).

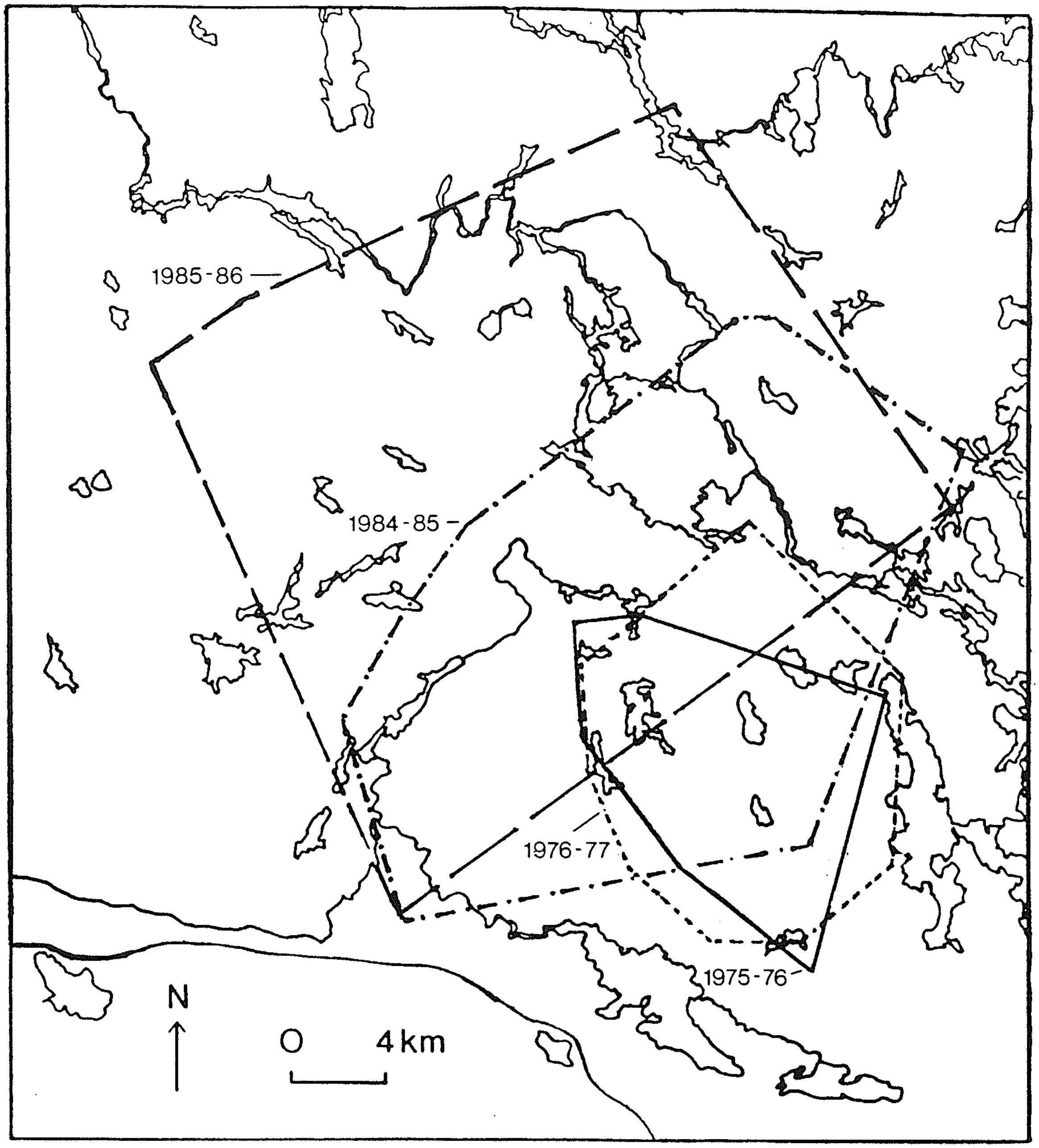

1985-86
1984-85
1976-77
1975-76
N
0 4 km

Figure 21. Sightings of caribou and their sign during winter aerial surveys 1984-85 in relation to the extent of the 1980 fire (hatched lines).

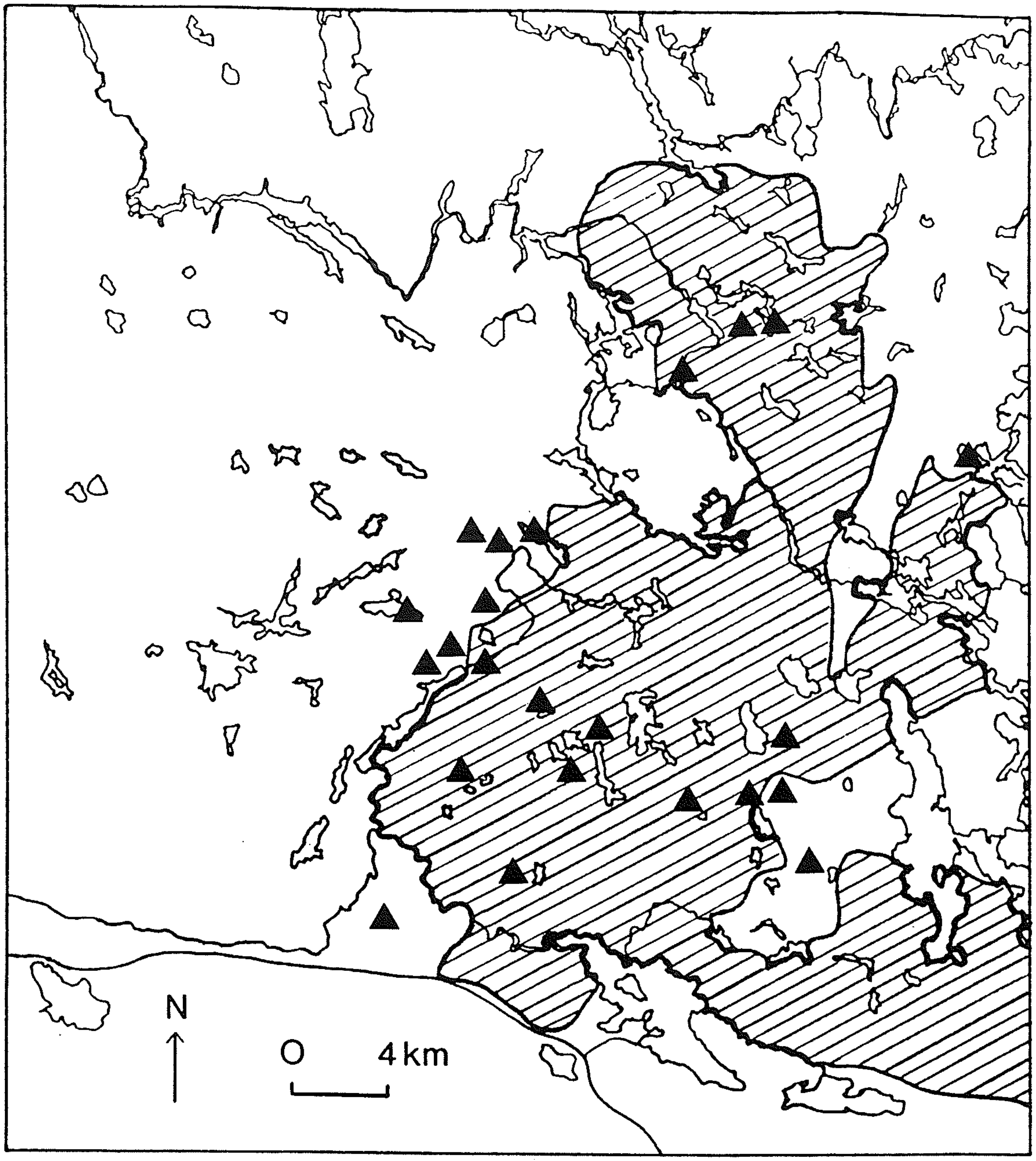
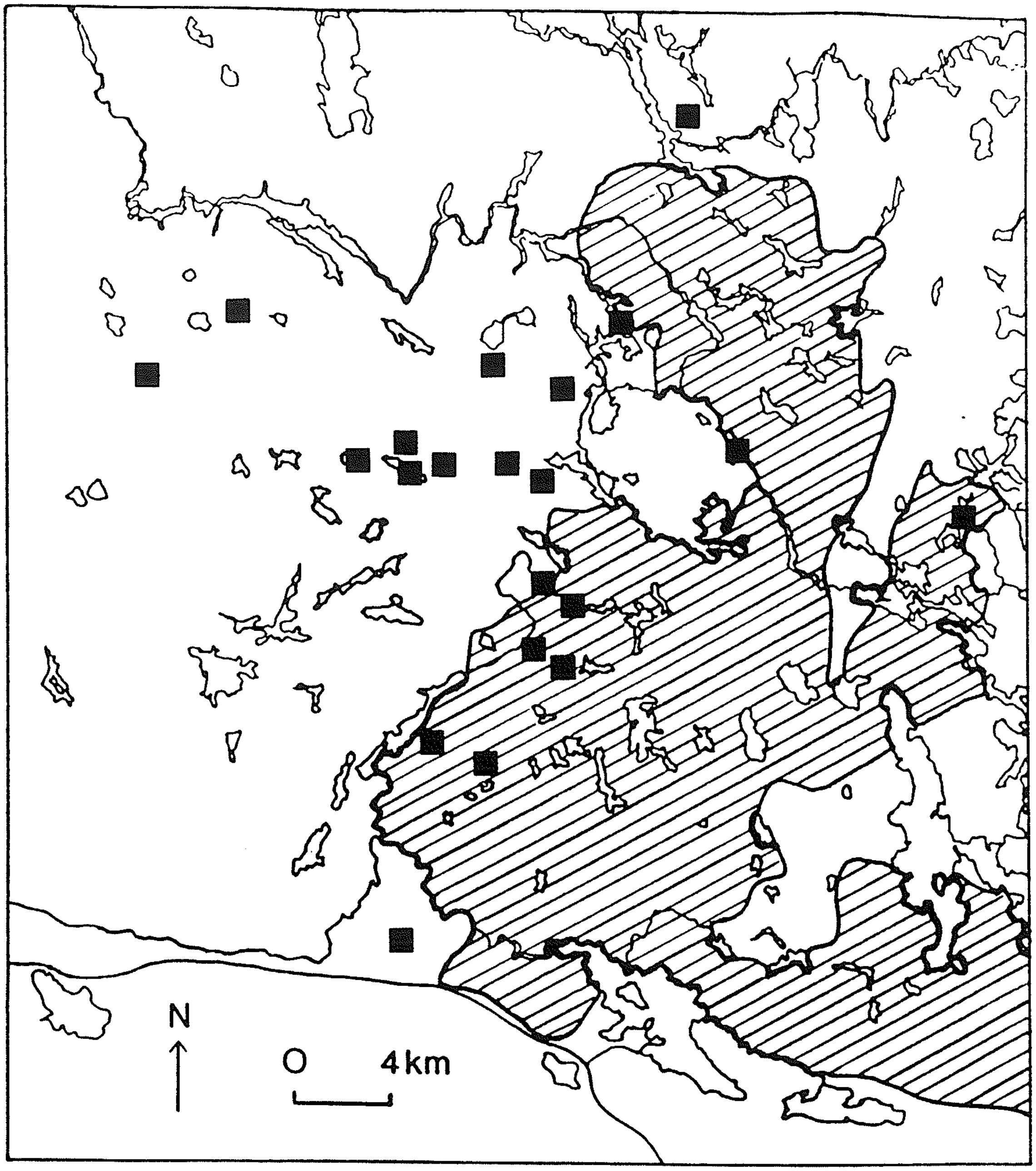

N
0
4km

Figure 22. Sightings of caribou and their sign during winter aerial surveys 1985-86 in relation to the extent of the 1980 fire (hatched lines).


N
O
4km

5. DISCUSSION

5.1 Fire and Plant Communities

Many authors (Kelsall et al. 1977, Miller 1980, Ohmann and Grigal 1981) have recognised the difficulty in generalising about the effects of wildfire in boreal ecosystems; because weather largely dictates fire severity and recovery, fires are seldom alike. Yet, as Alexander (1982: 355) has noted, many researchers tend to "...view fire as a binary event: an area burned or it did not." Broader understanding of the ecological impact of fire, then, must be founded on measurable traits of fire behaviour (Alexander 1982, Van Wagner 1983).

The extreme values of Duff Moisture Code (DMC) (Figure 4) and Buildup Index (BUI), and extensive ground investigations indicate that the 1980 Wallace Lake fire should be considered a 'severe' burn (sensu Wells et al. 1979, in Viereck and Schandelmeier 1980): loss of the duff and organic layer averaged about 10 cm in upland areas (unpublished TBS files). In comparison, Walker and Stocks (1972) found that the Whistle Lake fire in northern Ontario consumed about 70 % of the litter and duff at a DMC of 72.7. Methven et al. (1975), in the same region, noted BUI values of 36 to 74 corresponded to 'deeply burned' organic soils. At Wallace Lake BUI ranged from 108 to 147 in 1980.

The differential predisposition of sites to burn has resulted in a patchwork of burned and unburned habitats within the study area. This incomplete destruction of all stands has been noted elsewhere; LeResche et al. (1974) found that in Alaska only 53 % of the area within a 125,000 ha fire actually burned. Because resistance to combustion is not equally distributed across habitats, however, the intact portion of the study area is not simply a microcosm of the entire pre-fire range. In general, we can expect such wildfires to furnish caribou with intact bogs and burned uplands. Those uplands that survive will generally be small, widely-scattered islands and points due to the fortuitous interspersion of fire barriers.

The post-fire recovery of Wallace Lake habitats appears to be similar to analogous ranges in Ontario and Minnesota (Ahlgren 1960, Methven et al. 1975, Ohmann and Grigal 1979). These studies and others (Johnson 1981, Carleton 1982) suggest that the initial floristic arrangement is an important determinant for revegetation following fire. The present data agree; inter-community relationships, as indicated by the ordination of habitats, tend to persist after disturbance by fire. The fact that habitat distinctions are less pronounced is consistent with suggestions that other, stochastic factors (the proximity of a seed source, for example) also play an important role (Carleton 1982, Kenkel 1986).

It was considered, at the outset of this project, that 'mature' habitats had largely originated from the widespread 1895 fire in the region; comparative evaluation was based on analogous habitats through time. This habitat x age analysis is confounded, however, because some recognised types, rather than being perpetuated through time, are a consequence of time since burning. In particular, mixed coniferous (3) and some mixed deciduous (5) types appear to have originated at an earlier date, circa 1826.

Four mixed coniferous sites that were aged are consistent with this hypothesis. Further supportive evidence is as follows:

(1) At all mixed coniferous and most deciduous sites balsam fir makes a substantial contribution to the tree stratum. *Abies balsamea* is inevitably eliminated by fire (Day and Woods 1977) and is considered to be the only tree species capable of self-regeneration in the absence of fire (Carleton and Maycock 1978). Its presence should thus be indicative of older stands. In contrast, the species is absent from nearly all jack pine sites sampled.

(2) Habitats 3 and 5 commonly were found on islands and points, areas that may be expected to escape combustion for prolonged periods. Moreover, habitat 3 was concentrated only near Wallace and Obukowin lakes, and not distributed throughout the study area. It seems plausible that these discrete areas may have survived the 1895 fire entirely.

(3) Habitat 3 was virtually absent from the limits of the 1929 fire.

(4) No intermediate (37 year old) representatives of a mixed coniferous community exist, and only a small portion of this age of stand is mixed deciduous.

The evidence therefore suggests that mixed coniferous habitats are a later successional stage in the Wallace Lake region. Some mixed deciduous habitats (i.e. those with a Populus component) may also be involved. This mode of succession from jack pine to spruce-fir is similar to that hypothesised by Day and Woods (1977) for the Quetico region of Ontario. However, as the ordination of these habitats and other authors (Meeker and Merkel 1984, Kenkel 1986) suggest, succession and the tendency to evolve toward a similar community is complex, and depends on other, site-unique factors.

5.2 Plant Communities and Woodland Caribou:

5.2.1 Forage Quality and Quantity

That the quality of forages is largely commensurate with DMD appears valid for ruminants (Van Soest 1982, Robbins 1983). Yet one must recognise the limitations of inferring DMD of woodland caribou diets based on plant analytical fractions and published nutritional data. For instance, IVDMD and NBD are themselves only estimates. The digestibility of a heterogeneous diet, moreover, may not be predictable simply by the sum of its components (Blaxter 1962) (although preliminary results suggest this may hold true for Rangifer [Person et al. 1980b]). In any case, "... the only completely accurate way to evaluate a diet is to feed it to the animal itself" (Van Soest 1982: 76).

Nonetheless, estimates of the relative quality of taiga plants are likely valid. Significantly, those species deemed superior in digestibility (Appendix E) are the major items in the diet of Aikens caribou (Stardom 1977, Darby 1979, Table 6).

The effect of fire on the quality of forage for Aikens caribou is severe. Essentially, the replacement of terrestrial lichens with herbs and deciduous browse has resulted in a nutritional enhancement of summer range while causing a decline for winter. Clearly then, the implications of fire for range grazing capacity are contingent on the relative importance of summer and winter range to the well-being of woodland caribou.

Klein (1967, 1968) advanced the hypothesis that for holarctic ungulates, carrying capacity entails two different seasonal components: winter factors dictate the number of animals, while summer factors determine their physical condition. Klein and others have recognised, however, that summer and winter nutrition are not wholly unrelated; fat stores accumulated on high quality summer range may enhance winter survival, for example. Yet more recent data tend to conform to this dichotomous view of caribou-range interactions. White (1983) reported that doe milk production and fawn growth rates were highly correlated with the value of mid-summer habitat, irrespective of a high quality winter diet. On the other hand, Tyler (1986) concluded that winter forage availability was a more salient factor in overwintering survival of Svalbard reindeer (_R_._t_. _platyrhynchus_) than were autumn fat stores. Similarly, poor winter range in the form of low forage supply and severe nival conditions is responsible for high mortality of caribou when refuges are unavailable (Klein 1968, Parker et al. 1975, Reimers 1977).

The combustion of _Cladina_ lichens represents a critical loss from the winter forage supply of Aikens caribou. If winter range is the major determinant of populations levels, then caribou on burned-over ranges must compensate for the loss of this high-energy resource. We might expect this dietary adjustment to come from three sources: (1) a substitution of terrestrial lichens by using arboreal lichens from intact bog communities; (2) an increase in the intake of lower quality winter forage; or (3) accumulation of greater fat reserves derived from the abundant summer forages in most upland communities.

Arboreal lichens are often an important component in the diet of forest-dwelling caribou (Cringan 1956, Edwards and Ritcey 1960, Bergerud 1972, Scotter 1962, Helle 1981) and are apparently nutritionally similar to Cladina species (Scotter 1965, Thomas and Kroeger 1981, Thomas et al. 1984). Whereas other populations have been noted to switch to arboreal lichens under severe nival conditions, Aikens caribou exhibit the converse behaviour: bog habitats, the principal source of these pendulous lichens, contain significantly thicker and harder snowcover, particularly in late winter (Stardom 1975, Darby and Pruitt 1984; Api Conditions, Section 4.3). The higher energetic costs (Fancy and White 1987) of obtaining this more scattered forage, especially at the critical late-winter stage, almost invariably precludes it as an adequate substitute for terrestrial lichens.

To what extent could caribou meet their energetic requirements from the abundant but low-quality forages in burned areas? Well-documented for domestic ruminants is the relationship between DMD and energy intake: at low nutritive values, limitations in the rate of passage and the capacity of the gastro-intestinal tract combine to restrict intake (Blaxter et al. 1961, Conrad et al. 1964, Montgomery and Baumgardt 1965). Ammann et al. (1973) found this form of physical regulation occurred below 50 % DMD for white-tailed deer. Drodz (1979) found a similar relationship for roe-deer (Capreolus capreolus), and concluded that a minimum 58 % DMD was required to meet their maintenance energy requirements. The critical value for Rangifer has not as yet been determined; nonetheless, Syrjälä-Quist and Salonen (1983), in analysing 6 rations varying slightly in digestibility, suggested that DMD may be the limiting factor for energy intake in reindeer.

At the low end of forage quality spectrum, therefore, irrespective of forage abundance, we expect that caribou will have difficulty in meeting their energetic needs. No winter forages, except fungi and lichens, were estimated to be greater than 50 % digestible. The findings of White et al. (1981) agree: in a simulation study, two alternative feeding stategies were evaluated. One contained lichen and green material at moderate (45 %) DMD, but was of low availability (15 g $\cdot$ m^{-2}); the other was abundant dead plant material (31 % DMD at 100 g $\cdot$ m^{-2}). Neither strategy fulfilled more than 65 % of the animals' metabolic energy needs. These findings, in addition to the lack of significant amounts of senescent plant material in _Rangifer_ diets, suggest that Aikens caribou could not be sustained on burned ranges alone.

Alternatively, Aikens caribou might exploit superior summer ranges; hence dependence on winter range might be mitigated by the sufficient accumulation of fat reserves. The fire-caused enhancement of most summer habitats, however, is largely due to changes in _density_ rather than in the quality of forages. White et al. (1975) found that the theoretical intake of barren-ground caribou (_R.t. groenlandicus_) reached a plateau once live biomass exceeded about 50 g DM $\cdot$ m^{-2}. Results from the harvest sites indicate that approximately 60 % of the pre-fire range had an available dry matter biomass in excess of this threshold. This implies that neither the abundance nor the density of summer forages were limiting to Aikens caribou before the fire. Furthermore, the post-fire increase in density of forage beyond this point, without any substantial gain in quality, appears essentially superfluous unless Aikens caribou could devote more of their activity budget to foraging.

Reimers (1980) has hypothesised that adequate fat stores will develop only where caribou can allocate greater time to grazing and less energy on avoidance of man, predators, and insects. Prior to 1980, although Aikens caribou were non-migratory (Darby and Pruitt 1984) and not considered to be major items for wolves (Hill 1979), the potential for predation by wolves (Darby 1979), as well as occasional disturbance by man likely preclude Reimers' conditions. At least 6 wolves were noted to be present in the study area in December, 1985. Similarly, although caribou in the study area seem less subject to insect disturbance than barren-ground populations, their use of beaches in summer likely reflects attempts at insect relief (Darby 1979); insects appear to influence summer time budgets at the expense of grazing time. In fact, Reimers (1980) considered the necessary circumstances for independence of winter range to occur only on Svalbard. His hypothesis may extend to woodland caribou on the Slate Islands (Ontario): a viable population has existed there without mature forest, but, significantly, predators are also absent (Euler et al. 1976).

Nutritional aspects other than energy are worthy of mention here. Protein, in particular, is considered to be of significance for ungulate populations (Moen 1973, Mautz 1978). For caribou, protein may enhance the energy availability of a lichen diet (Person et al. 1980a). Boertje (1981) concluded that Denali caribou experienced a negative nitrogen balance during winter. A diet dominated by Cladina lichens, renowned for their poor N content (Scotter 1965, Pulliainen 1971, Parker 1975, Luick 1977, Boertje 1981, Appendix F), might be expected to subject caribou to protein deficiencies. Yet seldom are diets composed exclusively of lichens (Klein 1982). The ability of caribou to recycle urea (Hove and Jacobsen 1975, Wales et al. 1975), the moderate winter nitrogen content of evergreen and deciduous shrubs (circa 7 - 10 %), and their post-fire abundance suggests that the availability of protein is not limiting to Aikens caribou. Moreover, Syrjälä et al. (1980) found nitrogen balance of reindeer to be more strongly influenced by intake of energy than of digestible crude protein. In fact, although phenolic content might reduce the availability of protein for ruminants (Robbins et al. 1987), the moderate to high productivity of shrubs in bogs implies that the absolute abundance of protein *per se* has not been a crucial factor in the population's nutrition.

Finally, the energetic demands of woodland caribou and the resulting diet of lichens may also subject animals to mineral deficiencies (Staaland et al. 1982). In Finland, Hyvärinen et al. (1977) concluded that death of reindeer was due in part to mineral imbalances. Although wildfire might be expected to enhance availability of certain macro-elements in vascular plants, this benefit would almost assuredly be short-lived (Ohmann and Grigal 1979). The fragmentary understanding of this aspect of the nutritional ecology of *Rangifer* and the limited data available here make this effect difficult to assess.

5.2.2 Forage Accessibility

Much of the earlier work on snowcover and caribou ecology (Pruitt 1959, Henshaw 1968, Stardom 1975) was devoted to determinations of thresholds of sensitivity to api density, hardness, and thickness. While thresholds are indicative of the point at which caribou will seek more nivally suitable areas, these parameters do not act independently of one another. Stardom (1975), for example, recognised that the threshold for hardness exhibited by Aikens caribou will vary, depending on its vertical position in the api. Taken separately, therefore, thresholds may be inadequate for evaluating caribou winter range.

Pruitt's (1979) mathematical model, the Värriö Snow Index (VSI), is therefore significant in that it accounts for the interactive effects of hardness and thickness. The efficacy of VSI in modelling caribou winter activity has been demonstrated for several _Rangifer_ subspecies: _R_._t_. _tarandus_, _R_._t_. _groenlandicus_, and _R_._t_. _fennicus_ (Pruitt 1979, 1981, 1985, respectively). VSI also appears relevant to the ecology of woodland caribou (Habitat Utilisation, Section 4.5).

The energetics of locomotion by caribou under various nival conditions is not well understood at present. Data from studies of mule deer (_Odocoileus hemionus_), wapiti (_Cervus canadensis_) (Parker et al. 1984), white-tailed deer (Matfield in Fancy and White 1987) and caribou (Fancy and White 1987) agree, however: increased sinking depth relative to brisket height entails exponential increases in energy expenditure when walking through snowcover. Burned taiga habitats exhibit greater api thickness but are similar in hardness to unburned analogues through most of the winter season; this undoubtably places greater energetic stresses on Aikens caribou. By late winter, more severe ice crusts are additionally demanding: energy expenditure of travel through crusted snow was about twice that in uncrusted snow at the same sinking depth (Fancy and White 1987). Apparently shade and accumulation of qali ('snow on trees') by a mature overstory are important in providing an acceptable api substrate.

Extraction of forage from beneath the snowcover in burned areas may also impose increased costs. Significantly however, the api in jackpine communities, the major source of Cladina lichens, was less severely affected by fire than that in more closed-canopy types. Increases in thickness resulting from the removal of canopy cover is less here, consistent with the observations of Stevenson and Hatler (1985) that a compromise exists between overstory shelter and forage abundance. Nonetheless, harder late-winter crusts in all burned types would point to increased energetic costs of obtaining food by cratering (Thing 1977, Fancy and White 1985).

The increase in windfallen tree frequency is largely attributable to major summer windstorms after burning. In particular, strong gale winds caused a substantial blow-down on 8 August 1985, with similar events on 16 and 19 October 1984. Such step-wise accumulation is consistent with Schmid et al. (1985): beetle-killed ponderosa pine (Pinus ponderosa) were found to be resistant to windthrow for 2 years; thereafter, rate of fall was significant if winds exceeded 120 km $\cdot$ h^{-1}.

This dramatic build-up of obstacles implies added energy expenditure for locomotion through burned uplands. Logging slash, an analogous impediment, has been shown to be a significant factor affecting range use by other cervids

(Lyon and Jensen 1980, Wallmo and Schoen 1980). Parker et al. (1984) estimated that for mule deer and wapiti, cost of travel through logging slash increases due to depth and density of obstructions, particularly when depth exceeds 50% of brisket height. For Aikens caribou, downed timber at 0.5 to 1.0 m in height in burned areas would require jumping almost 5 times more frequently than in mature habitats when travelling in a straight-line fashion. Alternatively, animals could meander to avoid heavily-windblown pockets; nonetheless, as Parker and co-workers suggest, such avoidance of barriers in lieu of jumping would involve greater horizontal travel. The scope for such a strategy will undoubtably become more limited as the replacement stand ages and trees continue to fall.

5.2.3 Caribou Habitat Utilisation

Intensive tracking of Aikens caribou and the resultant indices of habitat use may suffer from several potential sources of bias: ground searches tended to follow bogs, lakes, and rivers, and were restricted in range; caribou may not defecate at a constant rate; feeding incidents are almost assuredly not equivalent in the biomass consumed. During aerial surveys, as well, caribou were theoretically four times more likely to be sighted in burns compared to closed-canopy forests. These biases may be at least partially counter-balanced by considering availability of habitats only within the ground search limits, and by following tracks over several kilometres across a diversity of plant communities.

Aikens caribou in their post-fire environment, nonetheless, exhibit patterns of winter habitat use largely parallel with that before the 1980 fire (Darby and Pruitt 1984), and consistent with observations on other taiga ranges (Simkin 1965, Fuller and Keith 1981, Edmonds and Bloomfield 1984). Selection of lowland habitats, in particular, is a seemingly common trait. As might be expected simply on the basis of increased availability, burned uplands are used significantly more than before the 1980 fire; however, consistent with Darby and Pruitt's findings, caribou still tend to exploit such areas disproportionately less than their occurrence. Stardom (1977) found winter ranges of several populations in eastern Manitoba to exclude stands less than 50 years old.

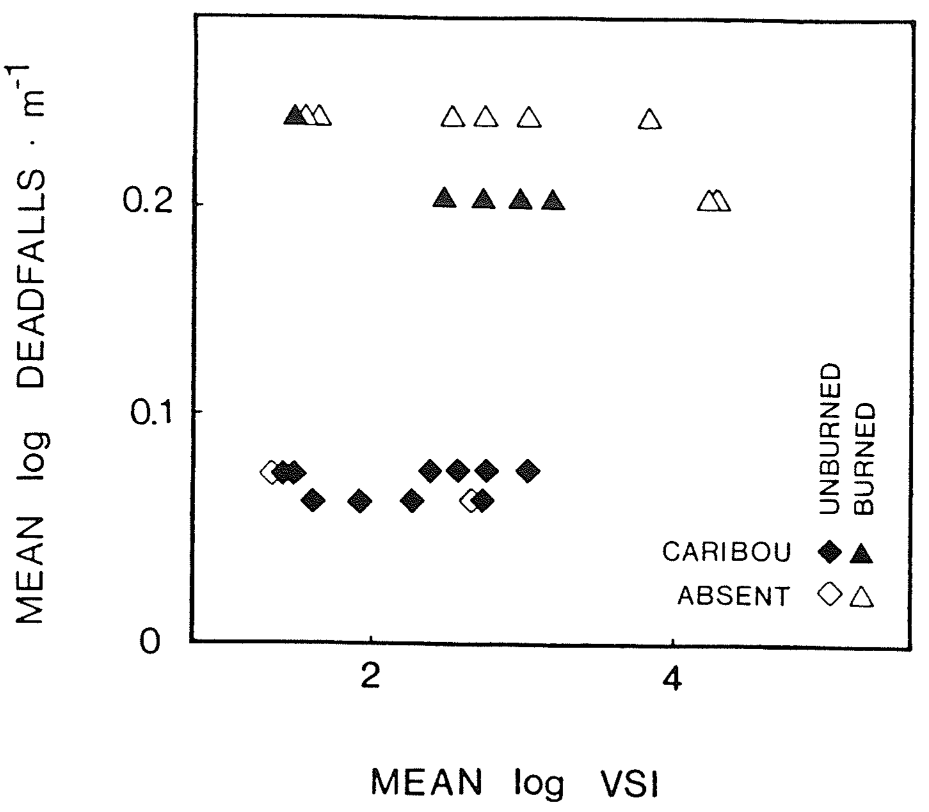
Significantly, preference for bogs and jack pine outcrops is in accordance with estimates of the quality and quantity of winter forages (Forage Productivity, Section 4.2). This supports earlier findings that caribou select habitats primarily for suitable forages and secondarily for acceptable nival conditions (Pruitt 1959, Bergerud 1974b). Use of lakes may be related to thinner snowcover (Darby and Pruitt 1984) or enhanced visibility of predators (Bergerud 1985), or both.

From the analysis of feeding sites, Aikens caribou appear to have maintained their dietary composition (Stardom 1977, Darby 1979) in spite of combustion of most of their winter range. Contrary to Bergerud (1972), exploitation of the fragmentary lichen crop that remains indicates that lichens are not only a principal forage, but are almost certainly preferred (sensu Petrides 1975).

Cessation of use of burned range contrasts sharply between the two winters of study. Yet this temporary abandonment of range does not appear attributable solely to aggravated api conditions or accumulated deadfalls. In 1985-86, the shift exclusively to unburned habitats occurred earlier but at a lower VSI than in the previous year. The discrepancy in VSI between burned and unburned regions, furthermore, was more accentuated in the first winter. Similarly, increase in deadfalls over this period cannot account for early-winter use of burns during 1985-86. An alternative hypothesis, that the abandonment of the burn is linked to exhaustion of lichen resoures, is not tenable: caribou were noted (on at least 3 occasions) to have reoccupied the 1980 burn during winter 1986-87 (unpublished TBS files).

Figure 23 considers this distinction between utilisation of upland communities: a synergistic effect of snowcover and windfallen trees is implicated. Deadfalls, insufficient in themselves in deterring caribou from burned range, apparently are capable of lowering the tolerance to

Figure 23. Winter utilisation of upland communities during 1984-85 and 1985-86 in relation to mean log deadfall frequency and weighted mean of log VSI. 'Unburned' stands refer to those of 55 years of age or greater.


MEAN log DEADFALLS · m^{-1}
0
0.1
0.2
2
4
MEAN log VSI
UNBURNED
BURNED
CARIBOU ◆ ▲
ABSENT ◇ △

nival conditions. This interaction can be synthesised into a single evaluative equation, derived from the canonical discriminant procedure, termed an 'api-deadfall index':

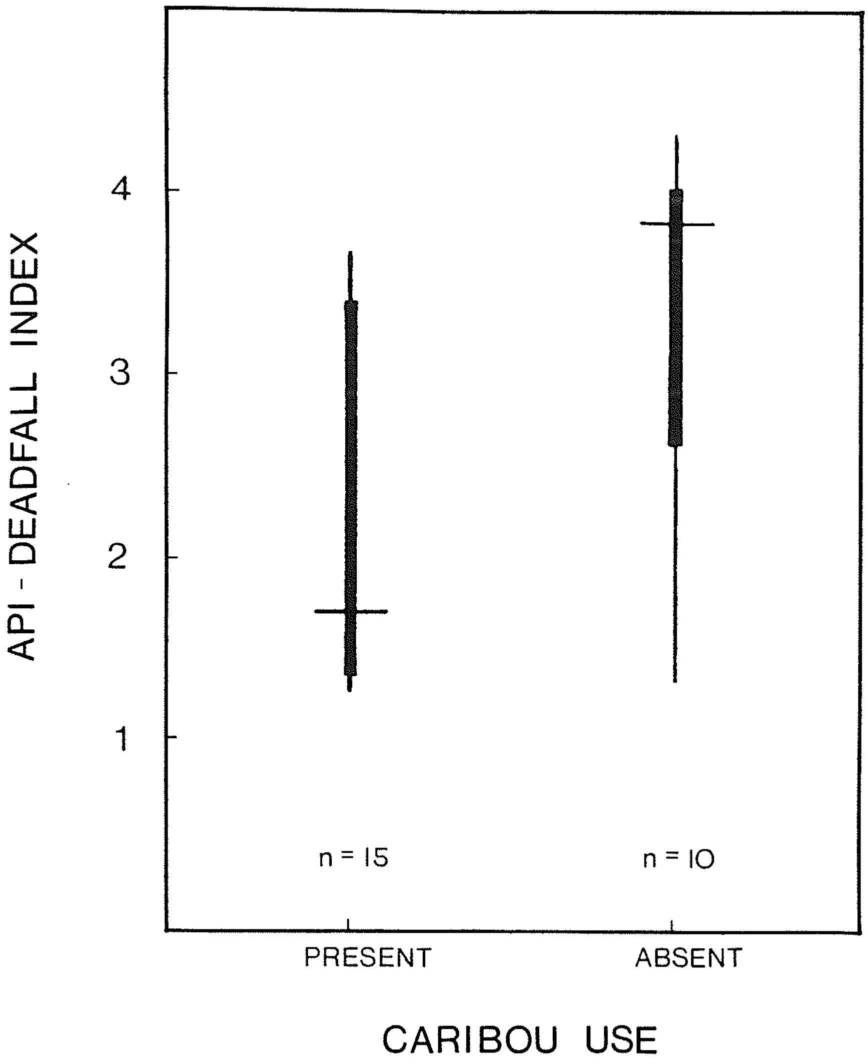
$$\text{index} = 12.96 \log (\text{deadfalls}) + 0.29 \log (\text{VSI})$$

where deadfalls = mean deadfall frequency per metre + 1
VSI = mean Värriö Snow Index weighted by habitat type.

This index distinguishes between use and non-use of taiga range by Aikens caribou (Figure 24). The multivariate F procedure indicates that this separation is significant, although mariginally so ($F_{2,22} = 4.497$, $0.01 < p < 0.05$). Admittedly, sample size is small and measures of windfallen tree frequency crude. Yet the index withstands testing from 1985-86 tracking results: discriminant analysis suggests that of two instances where caribou avoided burned ridges, one could be categorised as 'caribou absent'; more significantly, the actual routes utilised ($n = 3$) were all considered to be in the 'caribou present' category. Furthermore, selection for unburned uplands, expressed in 1985-86 but not in the previous winter, is consistent with this hypothesis.

Progressive non-use of the Wallace Lake burn is consistent with earlier observations by Klein (1971) and Skogland (1986), that for Rangifer, "... abandonment of range may result gradually from the cumulative effect of adverse stimuli" (Darby and Duquette 1986). Similarly,

Figure 24. Values of 'Api-deadfall Index' in relation to caribou presence and absence in upland communities. Ranges (vertical lines), medians (horizontal lines) and interquartile distances (solid lines) are indicated.


API - DEADFALL INDEX
4
3
2
1
n = 15
n = 10
PRESENT
ABSENT
CARIBOU USE

Wickstrom et al. (1984) modelled the foraging energetics of mule deer and wapiti; synergisms, more so than single factors, were implicated as the important consequences of range alteration. For woodland caribou, apparently the accumulation of deadfalls and snowcover is a sufficient hinderance to cause an abandonment of their burned, pre-fire range.

5.3 Fire and Woodland Caribou

Loss of food resources is an obvious and immediate result of fire on woodland caribou range. While this 'sudden fury of destruction' (Edwards 1954: 523) is pronounced, fire cycles of 50 to 100 years on similar taiga ranges (Heinselman 1973) imply that the effects of burning will extend beyond early-successional stages. The distinction between immediate and long-term consequences is crucial. Klein (1982: 393) wrote: "A major problem in assessing the relationship between fire and caribou ecology has been the failure to distinguish between short-term versus long-term effects."

Five years after burning, the measures of quantity, quality, and accessibility of forage largely agree: the Wallace Lake fire has effected a decline in the grazing capacity of taiga range vis à vis its pre-fire condition. In particular, the dismissal of lichens as a necessary dietary item (Skoog 1968, Bergerud 1974a, 1977) appears, in retrospect, to have been premature. Oft-cited are cases where animals have lost weight on an ad libitum diet of lichen (Kelsall 1968, Bergerud 1974a, Jacobsen and Skjenneberg 1975); yet as Klein (1982) argues, it does not follow that lichens are nutritionally unessential: even on a high plane of nutrition, weight loss is a universal adaptation to winter for holarctic cervids (Moen 1973, Mautz 1978). Moreover, the low protein content of lichens may be counter-balanced by abundant deciduous and evergreen shrubs, regardless of fire occurrence (discussed previously). In contrast, the loss of lichens as digestible carbohydrate is not readily compensated.

An underlying assumption here concerns the importance of range condition in determining caribou population status. Whether or not the short-term detriments of fire are realised seems to depend on the role of food in limiting woodland caribou populations. Darby (1979) observed no significant over-grazing of the pre-fire study area. Bergerud (1980, 1985) and Davis et al. (1978, 1983) have rejected the 'food limitation' hypothesis, and have advocated that predators largely set carrying capacity for caribou. Bergerud et al. (1983) summarised the argument:

> "... Carrying capacity for caribou herds with access to new ranges is not determined by food supplies, but rather is based on a more limiting need for space. This hypothesis states that a discrete caribou population co-existing with wolves requires a minimum of about 2 km^2 / caribou ... so that during the annual cycle interactions

> between caribou and wolves will be sufficiently infrequent that an adequate number of calves will live to equal the natural loss of adults."

In either case, the potential short-term detriments of fire for woodland caribou remain. Even if space rather than food resources is necessary for stable caribou populations, fire-caused accumulations of deadfalls and snowcover could confine caribou to undesirable densities unless refuges are available. The hypothesis of range limitation awaits adequate testing; of particular importance is the timing and duration when metabolic costs of foraging exceed its benefits. Nonetheless, on burned taiga range, the sparsity of adequate-quality forage relative to the costs of its procurement suggests that woodland caribou are food-limited.

Abandonment of range appears to be the fundamental adaptation of woodland caribou to the short-term effects of fire. Clearly then, access to adjacent lichen-dominated stands is essential. Results from Stardom (1977) suggest that forests in southeastern Manitoba will not achieve suitability as woodland caribou winter habitat until 50 years after burning. In intermediate condition (37 years), jack pine communities have recovered much of their original lichen biomass; yet the high density of young pine (Appendix B), not appreciably thinned in over a decade (Stardom 1977: 148), is apparently still sufficient to deter use of such habitats.

Api and windfallen trees appear to govern winter utilisation of burned taiga habitat. Full impact of fire, therefore, likely coincides with the maximum accumulation of deadfalls and/or exhaustion of remnant lichen stands. Contrary to Bergerud (1974a) then, demise of local caribou populations may not be realised until several years after fire. Edwards (1954), for instance, noted that woodland caribou in British Columbia declined about 9 years after a 1926 fire. On the other hand, the basis for the range fidelity of Aikens caribou, in spite of fire, is not clear; perhaps enhanced visibility of predators (Boonstra and Sinclair 1984) is related to this tenacity of pre-fire range.

These are short- and medium-term impacts of fire. If it is accepted that the tendency of upland communities is to evolve toward a spruce-fir mix (Fire and Plant Communities, Section 5.1), then the _absence_ of fire may also have important consequences for woodland caribou. By 160 years of age, such mixed coniferous habitats show increased feather moss cover at the expense of _Cladina_ lichens and other forage species. Consistent with Bergerud (1971) and Miller (1980), fire may have long-term benefits for the maintenance of forage productivity. It remains to be seen, however, how stands evolve beyond this 160-year period. In addition, these old-growth stands also exhibit the most favourable nival conditions, and thus may provide crucial late-winter shelter. Hence any decline in lichen availability in the absence of fire may be at least partially mitigated by lessening of energetic stresses from snowcover.

Balancing the severe, short-term detriments of fire against its less-salient, long-term benefits seems to be the key to the ecology of woodland caribou. Context is critical: the impact of wildfire -- whether population decline or shift to more favourable habitats -- will depend on local fire history, in particular the availability and size of lichen-dominated forests. In any case, the evolution of woodland caribou in a naturally fire-prone ecosystem suggests that successful co-existance is possible.

6. MANAGEMENT RECOMMENDATIONS

The following points are relevant for the management of woodland caribou in the East Lake Winnipeg area and on analogous taiga ranges:

1. Fire protection to provide adequate habitat.

Taiga in southeastern Manitoba and analogous ranges is not suitable to support woodland caribou in its early and intermediate seral stages (up to 50 years following fire). The priority for the range management of woodland caribou, therefore, must be to provide sufficiently-mature (> 50 years) habitat through fire protection. Data from Darby (1979) suggest that a minimum area of suitable winter range is 4 km^2 per caribou.

2. Delay in the impact of the short-term effects.

Following fire, the short-term deleterious effects on woodland caribou may not be immediate. This occurs because incomplete combustion of upland stands can be expected to provide some remnant lichen habitat; as well, deadfalls will not accumulate substantially for a few years. Therefore, five years or more may be required until the short-term detriments are realised.

3. Extension of fire protection to alternate ranges.

Woodland caribou appear to adapt to the short-term impact of fire by abandoning their range. Thus the presence of adjacent, lichen-abundant stands is crucial for the successful mitigation of these short-term effects. This implies that range protection must be afforded not only to existing woodland caribou range, but also to potential caribou habitat to permit a range shift in case of fire. For Aikens caribou, recent fires (1976 - 1987) have eliminated all such alternative habitat; thus the stands west of Leaf and Aikens lakes, originating in the 1929 fire, must be protected from fire until younger, adjacent stands have recovered (the year 2030).

4. Other human disturbances.

Less is known of the consequences of logging and other human disturbances on woodland caribou. Current knowledge from other cervids nonetheless suggests that range alterations are synergistically deleterious; such activities should thus be restricted on actual and potential Aikens caribou range until their impact -- particularly in light of the loss of range through recent fires -- has been clarified.

5. The importance of local fire history.

It is essential to distinguish between the short-term and long-term effects of fire. The absence of fire for 160 years may also have negative, although less salient, consequences. However, stands in excess of this age were not studied here, so this point requires clarification. At present, data suggest that small (< 40 km^2), lightning-inititated fires may be beneficial over the long term once taiga exceeds 150 years of age to optimise lichen productivity and habitat heterogeneity. In any case, providing adequate range of at least 50 years of age remains the priority in woodland caribou management, but must be implemented on the basis of local fire history.

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8. Appendices

Appendix A.

Species compostion of macroplots harvested during August/September 1985.

Table A.1. Species composition of harvest macroplots for habitat 1 (bog communities).

Community Type	Species	Frequency (percent)	Mean Density[a] (no · m^{-2})	Mean Production[b] (g · m^{-2})
mature (1a)	Ledum groenlandicum	72	90.00	7.76
	Gaultheria hispidula	50	1.00	1.59
	Vaccinium vitis-idaea	63	41.17	1.46
	Chamaedaphne calyculata	17	13.17	1.19
	Kalmia polifolia	17	3.67	0.22
	Oxycoccus species	37	1.54	0.21
	Smilacina trifolia	7	0.83	0.09
	fungi	3	0.33	0.04
	graminoids	8	0.21	0.04
	Cornus canadensis	2	0.17	0.01
	Cladonia species	2	0.04	0.00
	feather mosses	93	67.42	--
	Sphagnum species	38	23.29	--
mature (1a) [burnt]	Ledum groenlandicum	54	410.77	53.26
	Vaccinium vitis-idaea	62	186.62	6.73
	Chamaedaphne calyculata	35	52.46	3.89
	Smilacina trifolia	55	19.54	2.18
	Oxycoccus species	45	5.69	2.07
	Kalmia polifolia	9	11.08	0.56
	Populus species	5	1.54	0.15
	Epilobium angustifolium	6	1.08	0.10
	Vaccinium species	2	6.46	0.09
	Rubus chamaemorus	5	0.92	0.09
	fungi	20	8.00	0.02
	Peltigera species	8	0.19	0.02
	Marchantia polymorpha	11	1.38	0.01
	Misc. forbs	5	0.62	0.00
	Cladonia species	2	0.04	0.00
	Ceratodon purpureus	86	15.00	--
	Polytrichum species	91	13.19	--
	Sphagnum species	63	9.30	--
	feather mosses	17	0.81	--
intermed. 1b	Ledum groenlandicum	87	114.17	13.56
	Chamaedaphne calyculata	80	102.67	11.23
	Smilacina trifolia	82	47.50	6.83
	graminoids	90	7.96	4.84
	Kalmia polifolia	68	58.17	2.91
	Vaccinium vitis-idaea	32	42.83	1.98
	Andromeda polifolia	18	9.50	1.63
	Oxycoccus species	82	8.88	1.45
	Misc. shrubs	2	0.50	0.15
	Cladina species	2	0.25	0.09
	Equisetum species	2	0.17	0.08
	fungi	5	0.67	0.03
	Misc. forbs	2	0.17	0.00
	Cladonia species	2	0.04	0.00

Table A.1. (continued)

	Sphagnum species	100	87.79	--
	feather mosses	13	2.33	--
bog-forest (1d)	Alnus species	25	102.50	29.56
	Ledum groenlandicum	97	200.00	22.79
	Chamaedaphne calyculata	42	36.83	5.19
	Salix species	7	16.00	3.42
	Betula species	3	37.33	1.95
	Vaccinium vitis-idaea	43	35.17	1.78
	graminoids	87	6.25	1.74
	Smilacina trifolia	18	5.00	0.57
	Equisetum species	8	0.83	0.39
	Vaccinium species	2	26.83	0.34
	Cornus canadensis	7	3.00	0.34
	fungi	8	1.50	0.28
	Oxycoccus species	22	1.38	0.28
	Rubus species	8	1.50	0.20
	Spirea alba	2	2.17	0.15
	Rubus idaeus	3	1.00	0.15
	Waldsteinei fragariodes	12	5.33	0.12
	Trientalis borealis	17	2.83	0.09
	Gaultheria hispidula	15	0.38	0.07
	Pyrola species	12	3.67	0.05
	Misc. forbs	8	2.17	0.05
	Clintonia borealis	2	0.17	0.04
	ferns	2	0.17	0.03
	Coptis trifolia	3	1.17	0.01
	Sphagnum species	100	75.17	--
	feather mosses	100	0.25	--
semi-open (1e)	Chamaedaphne calyculata	98	347.25	17.67
	Kalmia polifolia	98	360.59	15.48
	graminoids	90	7.70	6.52
	Andromeda glaucophylla	78	75.88	6.39
	Oxycoccus species	100	19.31	3.68
	Smilacina trifolia	73	22.35	2.98
	Ledum groenlandicum	53	33.14	2.25
	fungi	6	1.57	0.14
	Misc. shrubs	10	0.98	0.14
	Vaccinium vitis-idaea	2	3.73	0.11
	Sphagnum species	100	94.66	--
	Polytrichum species	12	0.98	--
sedge meadow (1f)	graminoids	100	21.04	93.63
	Salix species	60	419.79	33.06
	Myrica gale	29	136.88	15.08
	Alnus species	4	26.04	2.02
	Potentilla palustris	25	6.67	1.50
	Betula species	2	11.25	0.62
	Spirea alba	2	4.17	0.37
	fungi	2	0.42	0.00

Table A.1. (continued)

Waldsteinei fragariodes	2	0.21	0.00
Mnium species	35	3.96	--
feather mosses	8	0.47	--

[a] Stands were in mature (90+ year) condition unless otherwise stated. Burnt stands were 5 years of age.

[b] Percent cover for mosses, graminoids, lichens, and creeping shrubs (see Methods).

[c] Air dry weight. Production was estimated as 10% and 50% of biomass for lichens and some perennials respectivity. (See Methods).

Table A.2. Species composition of harvest macroplots for habitat 2 (jack pine sandplain).

Age	Species	Frequency (percent)	Mean Density[a] (no · m^{-2})	Mean Production[b] (g · m^{-2})
mature	Arctostaphylos uva-ursi	75	123.88	11.03
	Vaccinium species	78	429.88	6.50
	Vaccinium vitis-idaea	86	109.38	5.59
	Lycopodium complanatum	26	13.25	3.30
	Maianthemum canadense	80	37.84	2.13
	Linnaea borealis	71	8.34	1.44
	Chimaphila umbellata	29	5.38	0.72
	Aralia nudicaulis	13	1.25	0.66
	Cornus canadensis	18	3.63	0.52
	Cladina species	21	1.44	0.46
	Clintonia borealis	4	0.75	0.36
	Potentilla tridentata	6	1.13	0.05
	fungi	6	1.88	0.01
	Cladonia species	3	0.06	0.01
	Gaultheria hispidula	1	0.03	0.01
	graminoids	1	0.03	0.00
	Juniperus species	3	0.38	--
	feather mosses	100	88.94	--
	Polytrichum species	1	0.03	--
intermed.	Linnaea borealis	53	6.16	1.08
	Arctostaphylos uva-ursi	9	5.75	0.54
	Vaccinium species	16	25.00	0.51
	Chimaphila umbellata	18	2.75	0.41
	Maianthemum canadense	26	8.38	0.38
	Cornus canadensis	19	3.25	0.30
	Rosa species	9	2.25	0.27
	Aralia nudicaulis	5	0.50	0.22
	Pyrola species	9	1.63	0.15
	Cladina species	16	1.03	0.08
	Cladonia species	26	0.97	0.05
	fungi	20	3.88	0.03
	Corylus species	1	0.50	0.03
	Misc. forbs	4	0.50	0.02
	Peltigera species	3	0.06	0.01
	feather mosses	100	80.56	--
	Polytrichum species	1	0.03	--
burnt	Vaccinium species	85	721.25	10.63
	Cornus canadensis	96	119.88	10.41
	Lycopodium complanatum	63	45.88	6.96
	Arctostaphylos uva-ursi	26	44.50	3.84
	Rosa species	15	10.63	2.96
	graminoids	48	2.88	2.87
	Galium species	59	35.75	2.61
	Fragaria species	41	41.88	2.45
	Apocynum species	15	1.88	2.40
	Potentilla tridentata	39	21.13	2.32

Table A.2. (continued)

Linnaea borealis	51	6.97	2.02
Maianthemum canadensis	65	25.13	1.19
Misc. forbs	44	14.13	1.09
Aralia nudicaulis	25	3.88	0.90
Amelanchier alnifolia	10	9.88	0.86
Symphoricarpos albus	13	16.38	0.64
Diervilla lonicera	3	0.38	0.57
Leguminosae	45	8.13	0.49
Clintonia borealis	4	1.25	0.34
Pyrola species	16	4.25	0.28
Rubus species	13	2.00	0.25
Spirea alba	9	2.88	0.24
Corylus americana	1	1.88	0.24
Ledum groenlandicum	3	1.50	0.21
Chimaphila umbellata	5	1.25	0.17
Epilobium angustifolium	10	1.13	0.13
Aralia hispida	4	0.50	0.11
Rubus idaeus	4	0.75	0.06
Trientalis borealis	4	0.88	0.05
Misc. forb	1	0.13	0.02
Vaccinium vitis-idaea	1	0.13	0.01
Polytrichum species	83	10.28	0.00
fungi	1	0.13	0.00
Ceratodon purpureus	81	5.88	--
feather mosses	8	0.66	--

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[a] 'Mature' refers to stands of at least 90 years, 'intermediate' to those 37 years, and 'burnt' to those 5 years of age.

[b] Percent cover for mosses, graminoids, lichens, and creeping shrubs (see Methods).

[c] Air dry weight. Production was estimated as 10% and 50% of biomass for lichens and some perennials respectively. (See Methods).

Table A.3. Species composition of harvest macroplots for habitat 3 (mixed coniferous forest).

Age	Species	Frequency (percent)	Mean Density[a] (no. $\cdot m^{-2}$)	Mean Production[b] (g $\cdot$ m^{-2})
mature	Cornus canadensis	25	7.88	0.94
	Aralia nudicaulis	14	1.75	0.67
	Lycopodium complanatum	11	2.75	0.47
	Lycopodium annotinium	13	12.00	0.42
	Maianthemum canadensis	30	19.19	0.41
	Lycopodium obscurum	6	0.88	0.25
	Coptis trifolia	19	14.13	0.22
	Clintonia borealis	6	0.88	0.22
	fungi	14	2.00	0.08
	Linnaea borealis	6	0.31	0.06
	Trientalis borealis	13	1.38	0.05
	Rubus species	5	0.50	0.05
	Pyrola species	4	0.63	0.04
	Rosa species	1	0.50	0.04
	Equisetum species	1	0.13	0.04
	Vaccinium species	3	1.38	0.02
	Peltigera species	1	0.19	0.01
	Diervilla lonicera	1	0.25	0.01
	Cladonia species	11	0.28	0.01
	Cladina species	1	0.03	0.00
	Corylus americana	1	0.13	0.00
	Betula species	1	0.13	0.00
	feather mosses	99	56.00	--
burned	Populus species	13	110.63	24.74
	Epilobium angustifolium	64	11.00	17.99
	Rubus idaeus	73	27.88	6.78
	Cornus canadensis	54	53.00	5.07
	graminoids	34	3.00	3.48
	Equisetum species	23	5.00	1.43
	Salix species	4	8.13	1.08
	Leguminosae	11	1.63	1.05
	Rosa species	4	5.50	0.65
	Vaccinium species	4	34.25	0.51
	Diervilla lonicera	5	1.38	0.47
	Polygonum cilinode	21	4.00	0.29
	Ribes species	1	0.88	0.24
	Prunus species	4	0.50	0.18
	Aralia nudicaulis	4	0.38	0.15
	Linnaea borealis	1	0.19	0.14
	Aralia hispida	8	1.00	0.13
	Pyrola species	3	1.88	0.08
	Petasite palmatus	1	0.13	0.02
	Peltigera species	10	0.25	0.02
	Coptis trifolia	1	0.75	0.01
	Polytrichum species	90	18.72	0.00
	Marchantia polymorpha	4	0.50	0.00
	Compositae	1	0.25	0.00

Table A.3. (continued)

Misc. forbs	1	0.13	0.00
feather mosses	4	0.53	--
Ceratodon purpureus	95	18.09	--

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[a] 'Mature' refers to stands of at least 90 years, 'intermediate' to those 37 years, and 'burnt' to those 5 years of age.

[b] Percent cover for mosses, graminoids, lichens, and creeping shrubs (see Methods).

[c] Air dry weight. Production was estimated as 10% and 50% of biomass for lichens and some perennials respectively. (See Methods).

Table A.4. Species composition of harvest macroplots for habitat 4 (jack pine outcrop).

Age	Species	Frequency (percent)	Mean Density[a] (no · m^{-2})	Mean Production[b] (g · m^{-2})
mature	Cladina species	91	29.91	14.34
	Arctostaphylos uva-ursi	25	47.63	3.43
	Vaccinium species	31	199.63	2.85
	Salix species	1	18.38	2.22
	Diervilla lonicera	9	6.38	2.20
	Amelanchier alnifolia	8	17.50	1.22
	ferns	6	4.13	0.59
	Potentilla tridentata	25	10.38	0.57
	Maianthemum canadense	21	7.50	0.43
	Prunus species	1	6.13	0.37
	graminoids	16	0.41	0.22
	Linnaea borealis	11	1.06	0.21
	Umbilicaria species	13	1.09	0.18
	Chimaphila umbellata	1	0.38	0.13
	Peltigera species	3	0.50	0.07
	Cladonia species	54	1.34	0.06
	Fragaria species	1	1.00	0.05
	Aralia nudicaulis	1	0.13	0.04
	Stereocaulon species	5	0.13	0.01
	Misc. forbs	3	0.38	0.00
	fungi	3	0.25	0.00
	Clintonia borealis	1	0.13	0.00
	Juniper species	1	0.13	--
	feather mosses	99	38.50	--
	Polytrichum species	1	0.03	--
	Sphagnum species	1	0.03	--
intermed.	Cladina species	76	23.09	11.77
	Vaccinium species	21	76.75	1.86
	Prunus species	1	1.00	0.86
	graminoids	13	1.06	0.80
	Polygonum cilinode	6	1.00	0.80
	Cladonia species	84	3.66	0.64
	Stereocaulon species	51	2.53	0.49
	Potentilla tridentata	4	2.75	0.45
	Umbilicaria species	38	1.56	0.19
	Corydalis sempervirens	4	0.75	0.19
	Spirea alba	4	1.25	0.14
	Misc. forbs	3	0.63	0.10
	Campanula rotundifolia	1	0.38	0.07
	fungi	8	1.38	0.05
	Linnaea borealis	4	0.41	0.03
	Cornus canadensis	1	0.13	0.01
	Maianthemum canadense	1	0.19	0.01
	Peltigera species	1	0.03	0.00
	feather mosses	54	16.56	--
	Polytrichum species	48	6.28	--

Table A.4. (continued)

burnt	Vaccinium species	6	80.63	1.46
	graminoids	6	0.59	0.67
	Populus species	3	3.13	0.61
	Aralia hispida	5	0.63	0.27
	Ledum groenlandicum	1	1.88	0.19
	Salix species	1	0.38	0.15
	fungi	6	1.25	0.14
	Fragaria species	1	1.25	0.12
	Epilobium angustifolium	1	0.13	0.10
	Misc. forbs	4	1.13	0.03
	Compositae	3	0.25	0.02
	Ceratodon purpureus	66	15.00	--
	Polytrichum species	39	5.38	--
	feather mosses	1	0.03	--

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[a] 'Mature' refers to stands of at least 90 years, 'intermediate' to those 37 years, and 'burnt' to those 5 years of age.

[b] Percent cover for mosses, graminoids, lichens, and creeping shrubs (see Methods).

[c] Air dry weight. Production was estimated as 10% and 50% of biomass for lichens and some perennials respectively. (See Methods).

Table A.5. Species composition of harvest macroplots for habitat 5 (mixed deciduous-coniferous forest).

Age	Species	Frequency (percent)	Mean Density[a] (no · m^{-2})	Mean Production[b] (g · m^{-2})
mature	Diervilla lonicera	63	36.00	11.90
	Cornus canadensis	76	30.25	3.08
	Corylus americana	4	7.25	2.50
	Clintonia borealis	44	8.38	1.88
	Shepherdia canadensis	3	16.13	1.77
	Ledum groenlandicum	11	12.75	1.25
	Lycopodium annotinium	25	24.38	1.06
	graminoids	43	1.84	0.95
	Aralia nudicaulis	13	1.75	0.75
	Rubus species	28	5.38	0.66
	Vaccinium species	19	37.25	0.56
	Rosa species	4	1.63	0.54
	Maianthemum canadense	31	6.28	0.34
	Amelanchier alnifolia	3	3.13	0.32
	Lycopodium obscurum	8	2.13	0.30
	Petasites palmatus	6	1.38	0.25
	Fragaria species	13	4.50	0.22
	Linnaea borealis	28	1.47	0.19
	Pyrola species	21	3.88	0.19
	Apocynum species	1	0.13	0.12
	Chimaphila umbellata	9	1.63	0.11
	Betula species	3	1.88	0.11
	Epilobium angustifolium	1	0.13	0.09
	Streptopus roseus	4	0.38	0.08
	Mitella nuda	10	3.88	0.07
	fungi	9	1.13	0.04
	Trientalis borealis	8	0.75	0.04
	Leguminosae	8	0.75	0.04
	Rubus idaeus	1	0.38	0.04
	Galium species	3	0.38	0.03
	Populus species	1	0.13	0.03
	Salix species	1	0.13	0.03
	Peltigera species	9	0.22	0.02
	Misc. forbs	10	1.00	0.02
	Coptis trifolia	1	0.50	0.01
	Cladonia species	8	0.19	0.01
	Cladina species	1	0.03	0.00
	Smilacina trifolia	1	0.13	0.00
	feather mosses	91	24.53	--
	Polytrichum species	1	0.03	--
intermed.	Linnaea borealis	70	10.72	2.22
	Rosa species	14	5.50	1.36
	Fragaria species	64	53.63	1.16
	Cornus canadensis	26	7.00	0.67
	Epilobium angustifolium	3	0.50	0.59
	Pyrola species	28	8.00	0.57
	Mitella nuda	41	33.25	0.53
	Rubus species	20	3.25	0.53
	graminoids	8	0.19	0.40

Table A.5. (continued)

	Cornus stolonifera	4	0.88	0.28
	Viburnum species	4	1.50	0.26
	fungi	18	3.25	0.21
	Leguminosae	4	0.38	0.18
	Maianthemum canadense	10	1.00	0.08
	ferns	4	1.13	0.07
	Peltigera species	11	0.59	0.06
	Misc. forbs	4	0.63	0.05
	Symphoricarpus alba	5	2.00	0.04
	Aralia nudicaulis	1	0.13	0.04
	Cladonia species	24	0.59	0.03
	Cladina species	5	0.13	0.03
	Ribes species	4	0.88	0.03
	Misc. forb	1	0.13	0.03
	Petasites palmatus	1	0.25	0.02
	Diervilla lonicera	1	0.13	0.02
	Trientalis borealis	4	0.50	0.01
	Misc. shrubs	1	0.13	0.01
	Galium species	5	0.88	--
	feather mosses	84	11.88	--
burnt	Populus species	31	286.75	74.79
	Epilobium angustifolium	64	16.38	23.41
	Apocynum species	10	1.38	5.58
	Diervilla lonicera	9	11.88	4.34
	Rosa species	29	16.13	4.13
	Cornus canadensis	61	32.38	2.89
	Rubus species	38	14.63	2.46
	Equisetum species	21	5.50	1.77
	Leguminosae	35	6.00	1.15
	Petasites palmatus	39	10.38	1.06
	Galium species	13	4.75	0.79
	Rubus idaeus	8	3.50	0.61
	graminoids	18	0.59	0.54
	Pyrola species	21	4.00	0.42
	Lycopodium complanatum	6	2.63	0.34
	Streptopus roseus	4	1.25	0.32
	Misc. forb	18	2.88	0.26
	Clintonia borealis	5	0.50	0.26
	Salix species	3	0.38	0.24
	Aralia nudicaulis	5	0.50	0.23
	Fragaria species	16	6.00	0.22
	Symphoricarpus alba	4	3.63	0.18
	Vaccinium species	8	8.50	0.17
	Amelanchier alnifolia	1	2.13	0.13
	Maianthemum canadense	18	2.06	0.12
	Peltigera species	18	0.75	0.06
	Linnaea borealis	3	0.06	0.04
	Polygonum cilinode	3	0.25	0.03
	Misc. forb	1	0.13	0.03
	Misc. forb	4	0.38	0.00
	Marchantia polymorpha	10	0.25	--

Table A.5. (continued)

Ceratodon purpureus	88	15.13	--
feather mosses	36	1.38	--
Polytrichum species	35	2.81	--

[a] 'Mature' refers to stands of at least 90 years, 'intermediate' to those 37 years, and 'burnt' to those 5 years of age.

[b] Percent cover for mosses, graminoids, lichens, and creeping shrubs (see Methods).

[c] Air dry weight. Production was estimated as 10% and 50% of biomass for lichens and some perennials respectively. (See Methods).

Appendix B.

Canopy compostion of harvest macroplots.

Table B.1. Canopy composition (stems x $10^3 \cdot ha^{-1}$) of harvest macroplots for upland habitats. Data from burned communities represent the pre-fire canopy.

Community Type	Age[b]	Pinus banksiana	Picea spp[a]	Abies balsamea[a]	Larix laricina	Populus spp	Betula papyr
jack pine sandplain 2	interm	3.60	0.91	0.00	0.00	0.00	0.23
	mature	0.91	0.26	0.00	0.00	0.00	0.00
	burnt	0.87	0.47	0.00	0.00	0.00	0.00
mixed coniferous 3	mature	0.08	0.38	1.17	0.00	0.02	0.02
	burnt	0.00	2.89	-	0.00	0.00	0.00
jack pine outcrop 4	interm	2.91	2.11	0.00	0.00	0.00	0.08
	mature	1.19	0.19	0.00	0.00	0.00	0.00
	burnt	0.02	1.40	-	0.00	0.00	0.00
mixed deciduous 5	interm	0.00	3.19	0.38	0.00	1.00	0.30
	mature	0.00	0.72	0.25	0.00	0.40	0.13
	burnt	0.02	1.23	-	0.00	0.34	0.00

[a] Balsam fir and spruce could not be distinguished in burned habitats and are placed together under Picea species.

[b] 'Mature' refers to stands of at least 90 years, 'intermediate' to those 37 years, and 'burnt' to those 5 years of age.

Table B.2. Canopy composition (stems x $10^3 \cdot ha^{-1}$) for bog community macroplots.

Community Type[a]	Pinus banksiana	Picea species	Abies balsamea	Larix laricina	Populus species	Betula papyr.
mature 1a (burnt)	0.00	3.60	0.00	0.00	0.00	0.00
mature 1a	0.00	6.40	0.00	0.00	0.00	0.00
intermediate 1b	0.00	3.68	0.00	0.02	0.00	0.00
bog-forest 1d	0.00	0.38	0.00	0.15	0.00	0.02
semi-open 1e	0.00	2.00	0.00	0.38	0.00	0.00
sedge meadow 1f	0.00	0.00	0.00	0.00	0.00	0.00

[a] Stands were in mature (90+ years) condition unless otherwise stated. 'Burnt' 1a bog was 5 years old.

Appendix C.

Biomass of arboreal lichens and related measures for intermediate (1b) and semi-open (1e) bogs.

Table C.1. Biomass of arboreal lichens and related measures for intermediate (1b) and semi-open (1e) bogs.

Community Type	No. of Trees Sampled	Mean Biomass[a] per 2 Branches (g)	Mean Branches per Segment	Trees per 400 m^2	Lichen Biomass[b] ($g \cdot m^{-2}$)
1e	24	0.60	6.88	126	2.10
1e	25	3.18	4.84	88	5.48
1e	27	1.00	5.59	127	2.87
1e	25	0.98	6.72	66	1.76
1b	25	2.25	10.56	111	10.67
1b	25	3.34	12.20	57	9.67
1b	24	1.00	6.96	71	2.00

[a] air-dry weight
[b] dry matter basis

Appendix D.

Example of the method employed for estimating digestibility of study area plant species.

Appendix D. Example of the Method for Estimation of Digestibility of Study Area Plant Species.

The following illustrates the method for inferring dry matter digestibility (DMD) of Wallace Lake plants from empirically-determined content of acid detergent fibre (ADF) and the DMD of caribou forages reported in the literature. Winter evergreen shrubs are used as an example.

Digestibility data for this group were compiled from the literature (Table D.1). The 20th and 80th percentiles of this reported range of DMD determined the lower and upper bounds for the estimated DMD of Wallace Lake species. For winter evergreen shrubs, therefore, the lower bound was 22.8 % DMD and the upper, 47.2 % DMD.

Because of the inverse relationship between ADF and DMD (White et al. 1975, Van Soest et al. 1978, Minson 1982), the Wallace Lake species with the highest ADF value, stems of Kalmia polifolia (74 %, Table E.2), was assumed to correspond to the lower bound of the reported DMD range (22.8 %). Similarly, Arctostaphylos uva-ursi, with a mean ADF of 28.2 %, had the highest estimated DMD of 47.2 %. All other species in the group were then assigned a DMD value using a reference equation that assumed a inverse linear relationship between ADF and DMD. The slope of this equation is therefore:

$$\frac{\Delta \text{ DMD}}{\Delta \text{ ADF}} = \frac{47.2 - 22.8}{28.2 - 74.0}$$

$$= -0.533$$

Therefore, the reference equation for winter evergreen shrub species is:

$$\text{DMD (estimated)} = 47.2 + 0.533\ (28.2 - \text{ADF})$$

For rarer species within the group (e.g. Gaultheria hispidula) where no ADF value was available, DMD was estimated simply as the median value (i.e. 34 %).

The same rationale was followed to determine reference equations for other study area plant groups. Groups with few collected representatives from the study area (i.e. lichens, graminoids, and winter forbs) were assigned their respective medians of reported DMD values.

Table D.1. Reported dry matter digestibility (DMD) of evergreen shrubs during winter. Collections were reported to have been made between October and March.

Species	DMD	Reference[a]
Ledum palustre, leaves	11.0	1
Dryas integrifolia, leaves	16.6	2
Andromeda polifolia, stems	27.0	3
Empetrum nigrum, leaves and stems	30.0	3
Chamaedaphne calyculata, stems	30.0	3
Ledum groenlandicum, stems	31.0	3
Vaccinium vitis-idaea, stems	34.0	3
Oxycoccus microcarpus, leaves and stems	34.0	3
Ledum groenlandicum, leaves	34.0	3
Vaccinium vitis-idaea, leaves	40.0	3
Andromeda polifolia, leaves	47.0	3
Chamaedaphne calyculata, leaves	48.0	3
Cassiope tetragona, leaves	49.1	2

[a] 1 = Boertje (1981); 2 = Thomas and Kroeger (1980); 3 = Thomas and Kroeger (1981).

Appendix E.

Dry matter nutrient content and estimated digestibility of study area plant species.

Table E.1. Dry matter nutrient content and estimated digestibility of plant species collected during July/August 1984 and August 1985. Samples consisted only of current year's growth unless otherwise indicated.

Growth Form	Species	Crude Protein[a]	ADF[b]	Ca	P	Estimated DMD[c]
decid. shrubs	Alnus spp.	17.8	46.2	0.54	0.07	57.2
	Spirea alba	9.3	46.8	0.61	0.10	57.4
	Salix spp.	11.1	43.7	1.00	0.15	58.2
	Populus spp.	11.3	43.4	1.30	0.16	58.3
	Myrica gale	12.9	42.8	0.34	0.09	58.5
	Rubus idaeus	7.3	37.5	1.06	0.31	60.6
	Vaccinium spp.	9.7	30.9	0.84	0.13	63.2
	Amelanchier spp.	10.7	29.4	1.28	0.46	63.8
	Betula spp.	13.2	28.7	0.68	0.11	64.1
	Rosa sp.	9.6	24.8	1.39	0.23	65.6
	Prunus spp.	12.3	23.9	1.50	0.44	66.0
	Diervilla lonicera	8.2	22.5	1.05	0.28	66.5
everg. shrubs	Andromeda glaucopylla	5.9	49.6	0.54	0.07	47.6
	Chamaedaphne calyculata	7.5	48.1	0.44	0.11	49.3
	Ledum groenlandicum	9.4	48.1	0.34	0.08	49.3
	[d]Oxycoccus sp.	5.9	41.3	0.88	0.09	57.1
	[d]Linnaea borealis	7.0	39.3	1.34	0.15	59.5
	[d]Gaultheria hispidula	6.6	39.2	0.93	0.12	59.6
	Kalmia polifolia	8.2	38.9	0.52	0.01	59.9
	Arctoshaphylos uva-ursi	5.4	35.0	0.82	0.11	64.4
herbs	Equisetum spp.	12.7	46.8	1.25	0.22	45.8
	Aralia nudicaulis	11.1	34.1	1.33	0.27	63.4
	Rubus spp.	9.9	33.2	1.09	0.26	64.7
	Cornus canadensis	10.0	33.0	2.79	0.28	65.0
	Epilobium angustifolium	8.5	30.5	1.18	0.29	68.5
	Maianthemum canadense	8.7	29.7	0.88	0.27	69.6
	Smilacina trifolia	20.9	26.7	0.46	0.28	73.7
	Fragaria spp.	9.7	25.6	1.65	0.34	75.3
	[d]Potentilla tridentata	7.8	25.5	1.17	0.23	75.4
	graminoids	10.1	45.6	0.24	0.13	56.7
lichen	[d]Cladina spp.	2.9	N/A	0.13	<0.05	62.0

[a] based on N x 6.25
[b] acid detergent fibre
[c] dry matter digestibility
[d] includes entire plant

Table E.2. Dry matter nutrient content and estimated digestibility of plant species collected during April 1986 and February 1987. Samples included only previous year's growth unless otherwise indicated.

Growth Form	Species	Crude Protein[a]	ADF[b]	Ca	P	Estimated DMD[c]
decid. shrubs	Alnus rugosa	10.3	41.3	0.70	0.15	48.6
	Populus sp.	7.0	42.5	1.02	0.14	47.3
	Salix sp.	6.1	51.0	0.45	0.11	38.0
	Betula glandulosa	6.7	53.5	0.37	0.08	35.3
	[e,f]Vaccinium sp.	4.3	59.7	0.39	0.08	27.8
	[d,f]Vaccinium sp.	4.9	61.0	0.48	0.07	27.8
	Rubus idaeus	5.8	63.5	0.37	0.11	24.4
everg. shrubs	[d]Arctostaphylos uva-ursi	5.6	27.7	0.64	0.11	47.2
	[e]Arctostaphylos uva-ursi	5.3	28.6	0.69	0.16	47.2
	Kalmia (leaves)	7.5	31.8	0.57	0.09	45.3
	[e,f]Vaccinium vitis-idaea	6.2	33.2	0.51	0.10	42.2
	Chamaedaphne (leaves)	8.0	33.4	0.59	0.10	44.4
	Andromeda (leaves)	5.9	39.8	0.64	0.06	41.0
	[d,f]Vaccinium vitis-idaea	5.9	41.8	0.51	0.09	42.2
	Ledum (leaves)	8.7	46.3	0.68	0.14	37.6
	Oxycoccus sp.	5.1	53.7	0.65	0.08	33.6
	Andromeda (stems)	4.3	57.7	0.23	0.06	31.4
	Ledum (stems)	5.1	60.3	0.71	0.10	30.0
	Chamaedaphne (stems)	4.6	64.4	0.23	0.07	27.9
	Kalmia (stems)	5.1	74.0	0.18	0.06	22.4
herbs	Cornus canadensis	7.3	26.3	2.46	0.22	27.9
	Epilobium angustifolium	4.3	50.5	1.38	0.06	27.9
	Equisetum sylvaticum	6.7	73.8	1.36	0.09	27.9
	graminoids	2.9	49.8	0.29	0.04	44.7
	graminoids	3.3	50.4	0.35	0.05	44.7

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[a] based on N x 6.25
[b] acid detergent fibre
[c] dry matter digestibility
[d] collected from unburned areas only; estimated DMD averaged from 2 samples
[e] collected from burned areas only; estimated DMD averaged from 2 samples
[f] includes entire plant

Appendix F.

Mean annual productivity of digestible dry matter for study area plant communities.

Table F.1. Mean annual productivity of digestible dry matter (DDM) for upland communities.

Season	Community Type	Age	Production of DDM ($g\cdot m^{-2}$) by digestibility class					
			<30%	30-40%	40-50%	50-60%	60-70%	>70%
summer	2	burnt	0.00	0.00	0.10	3.07	30.96	3.59
		interm.	0.00	0.00	0.00	0.87	1.67	0.03
		mature	0.00	0.00	0.00	4.41	16.29	0.05
	3	burnt	0.00	0.00	0.65	17.11	22.22	0.00
		mature	0.00	0.00	0.02	0.03	2.59	0.07
	4	burnt	0.00	0.00	0.09	0.82	1.19	0.22
		interm.	0.00	0.00	0.00	0.55	10.62	0.39
		mature	0.00	0.00	0.00	1.62	16.32	0.46
	5	burnt	0.00	0.00	0.81	44.07	33.12	0.17
		interm.	0.00	0.00	0.00	1.55	3.64	1.07
		mature	0.00	0.00	0.62	0.75	17.62	0.20
winter	2	burnt	11.95	2.74	3.11	0.00	0.00	0.00
		interm.	0.44	0.62	0.26	0.00	0.09	0.03
		mature	3.77	2.64	5.25	0.00	0.29	0.01
	3	burnt	8.99	1.17	13.26	0.00	0.01	0.00
		mature	1.07	0.04	0.00	0.00	0.01	0.07
	4	burnt	0.49	0.21	0.59	0.00	0.00	0.13
		interm.	0.79	0.61	0.36	0.00	8.12	0.05
		mature	1.26	2.33	1.73	0.00	9.09	0.00
	5	burnt	11.73	3.28	35.62	0.00	0.04	0.00
		interm.	1.26	1.48	0.18	0.00	0.08	0.19
		mature	2.82	6.64	0.44	0.00	0.02	0.04

Table F.2. Mean annual productivity of digestible dry matter (DDM) for bog communities.

Season	Community Type	Age	Production of DDM ($g \cdot m^{-2}$) by digestibility class					
			<30%	30-40%	40-50%	50-60%	60-70%	>70%
summer	1a	burnt	0.00	0.00	28.18	5.39	0.19	1.68
	1a	mature	0.00	0.00	4.41	2.04	0.01	0.11
	1b	mature	0.00	0.00	13.03	6.43	0.62	5.06
	1d	mature	0.00	0.00	13.98	21.18	2.18	0.67
	1e	mature	0.00	0.00	12.86	15.13	0.28	2.33
	1f	mature	0.00	0.00	0.00	82.51	1.43	0.00
winter	1a	burnt	4.27	17.94	1.40	0.00	0.01	0.02
	1a	mature	0.61	3.29	0.44	0.00	0.00	0.04
	1b	mature	3.95	5.00	6.93	0.00	0.52	0.02
	1d	mature	2.48	9.18	16.66	0.00	0.00	0.25
	1e	mature	3.64	1.88	15.25	0.00	0.19	0.13
	1f	mature	0.42	18.35	42.83	0.00	0.00	0.00

Appendix G.

Mean deadfall frequency for stands sampled during autumn 1985.

Table G.1. Mean deadfall frequency (number · m^{-1}) in relation to stacking height for stands sampled during autumn 1985.

Age of Stand (years)	Year of Most Recent Fires	n	Stacking Height of Bole (m)				
			0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5
burnt (9.5)	1976, 1895	12	1.288	0.135	0.023	0.004	0.000
burnt (5.5)	1980, 1929	12	0.469	0.123	0.037	0.008	0.003
burnt (5.5)	1980, 1895	22	0.606	0.152	0.044	0.013	0.003
mature (90+)	1895	14	0.101	0.034	0.011	0.002	0.000