THE UNIVERSITY OF MANITOBA

# SUBNIVEAN ACCUMULATION OF $CO_2$ AND ITS EFFECTS ON WINTER DISTRIBUTION OF SMALL MAMMALS

by

CHERYL EVELINE PENNY

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ABSTRACT

Measurements of subnivean $CO_2$ during two winters (1974 - 1975 and 1975 - 1976) in six different habitats in the taiga 280 km northeast of Winnipeg, Manitoba revealed that subnivean $CO_2$ accumulated consistently in four habitats while not in two others. The $CO_2$ concentrations increased up to maxima of five times ambient levels. The accumulation of $CO_2$ was affected primarily by density and hardness of the snow.

A reduction in small mammal numbers was associated with the fall critical period. Accumulation of subnivean $CO_2$ was frequently associated with changes in small mammal distribution, involving reductions in the numbers of animals present at the sites of greater $CO_2$ concentrations.

ACKNOWLEDGEMENTS

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At this time I would like to acknowledge the assistance of the following people without whose direction the project would not have got off the ground: Dr. D. Schindler, Dr. Neil Arnason, Dr. Terry Dick and especially Dr. W. O. Pruitt Jr. who created the Taiga Biological Station. Fellow students and friends such as Ed and Bonny Hill, Richard Leonard, Glenn Sutherland, Keith Yonge and Suzanne Levine were of great help. Especial thanks to Bill Conley and Don McDonald without whose support life would have been much more difficult, and lastly thanks to the many people who helped whenever they were up at Taiga Biological Station.

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# INTRODUCTION

A disagreement was found in the literature as to whether or not $CO_2$ increases in concentration or accumulates to levels greater than ambient (.03%/volume $CO_2$) under the snowcover and to what extent small mammal distributions are affected by such accumulations.

Bashenina (1956) found $CO_2$ levels concentrations increased up to 4% near Moscow . In the areas where greater concentrations of $CO_2$ were recorded she found subnivean mouse nests raised higher above the ground than in areas with lesser concentrations of $CO_2$. Pichler (in Geiger 1965) also mentioned that $CO_2$ was present in the subnivean area of a rye crop in concentrations greater than expected. Kelley et al (1968) and Kelley and Weaver (1969) studied $CO_2$ accumulation under the snow in the arctic tundra and quoted a range of 0.034 to 0.1 percent by volume $CO_2$. Havas and Mäenpää (1972) found subnivean $CO_2$ to accumulate to levels of .03 to 0.105 percent/volume in a *Hylocomium-Myrtillus* type forest in Finland.

In contrast, Fuller and Holmes (1972) stated that subnivean $CO_2$ did not increase sufficiently to affect small mammal distributions in taiga. Reiners (1968) found soil $CO_2$ production to be approximately zero in January in a cedar swamp, fen and oak forest. Kelley et al (1968) and Coyne and Kelley (1971) found subnivean $CO_2$ levels decreased to ambient once a snowcover of 20 cm. was established.

Therefore, the focus of this thesis is to answer the questions:

1. Does $CO_2$ accumulate in the subnivean space?
2. If it does, where and why do the accumulations occur?
3. Do any accumulations influence small mammal distributions?

$CO_2$ could accumulate by an increase either in production or in the strength of factors influencing retention. $CO_2$ is produced primarily by the decomposition of leaf litter and by plant and root respiration. It is also released from air pockets or reservoirs in the soil. Respiration form small mammals has been discounted as a significant contributor to amounts of subnivean $CO_2$ (Kelley et al 1968). Micro-organisms are the main decomposers of leaf litter (Benoit et al 1972) and have been shown to produce up to 28% of the $CO_2$ evolved on a woodland soil surface (Witkamp and Frank 1969).

Root respiration along with $CO_2$ released from small air pockets in the soil contributed the remaining 72% of $CO_2$ measured (Witkamp and Frank 1969). Root respiration was also reported by other authors as an important contributor (40.5%) of the over all $CO_2$ measured (Reiners 1968 Kosonen 1969, Brown and MacFayden 1969, and Anderson 1973). Root and micro-organism respiration are interrelated (r=0.72) with decomposition (Kucera and Kirkham 1971). Also, their combined contribution is the most significant in summer. Little soil testing has been conducted outside the summer months except for work done by Reiners

(1968). Therefore in winter another factor, plant respiration,may become more important. Both Hagerup (in Kalela 1962) and Havas and Mäenpää (1972) found significant plant respiration under the snow. So while one source of $CO_2$ may decline, another may increase in importance.

The production of $CO_2$ varies due to environmental conditions such as temperature, moisture levels, pH, wind as well as age and amount of litter. Many authors have found a positive correlation between plant or bacterial respiration and soil temperature, where respiration ceases at approximately $-7^{o}$C. (Flanagan and Scarborough 1972, Benoit et al 1972). However, the effect of temperature was observed only within critical limits of moisture, litter age and depth and all were interdependent (Witkamp 1963, 1966). The effect of pH on $CO_2$ production was evident only outside the range 5 to 7.5 (Flanagan and Scarborough 1972). Kelley et al (1968) found that wind negatively influenced $CO_2$ accumulation.

Differences from summer to winter in the distribution of small mammals have been noted by a number of authors (Iverson and Turner 1972, Beer 1961, Andrzejewski and Mazurkiewicz 1976, Kalela 1962, Buckner 1966, Riewe 1973 and Morris 1969). These differences are in response to changes in the environment (Stickel 1960, NcNab 1963). The subnivean environment is dark (Evernden 1966), with a relative humidity of 100%, quiet (Pruitt 1959a,1960), and has a relatively constant warm temperature (0 to $-7^{o}$C.) when compared to the supranivean environment (Pruitt 1957, Fuller et al 1969). Such a relatively constant environment develops when the snowcover reaches the hiemal threshold (15 to 20 cm.), and small mammals utilize or enter this as soon as it forms (Pruitt 1960). Without this environment small mammals could not survive northern winters (Pruitt et al 1961).

Once the hiemal threshold is established small mammals still can change their distributions within the habitat (West 1977). This distribution change is not necessarily correlated with temperature (Fuller 1977) or food availability (Gorecki and Gebczynska 1962, Grodzinski 1963, Chitty et al 1968, Flowerdew 1972, Andrzejewski and Mazurkiewicz 1976, Pernetta 1976, and Fairbairn 1977). Therefore something else in the subnivean environment may be triggering the changes in small mammal distribution.

Bashenina (1956) and others suggested $CO_2$ accumulation may influence small mammal distribution. The effect of $CO_2$ can be measured because small mammals respond by increased ventilation to increases in its concentrations (Galantsev and Tumanov 1969). The concentrations at which $CO_2$ could be detected by or affect small mammals is under study by a number of authors. Aquatic mammals have quite high tolerances to $CO_2$, with 10% causing little effect on ventilation or heart rates (Irving in Soholt et al 1973). Burrowing and hibernating mammals normally experience up to 2.5 to 3% by volume $CO_2$ in their chambers (Kennerly 1964, Studier and Proctor

1971, Williams and Rausch 1973). These concentrations are very high compared to the ambient levels. But, non-diving, non-fossorial, non-hibernating rodents have a much greater sensitivity to $CO_2$ (Soholt et al 1973, Darden 1971) and genera such as *Apodemus*, *Microtus* and *Clethrionomys* exhibited a reduction in heart rate of 12 to 25% when exposed to $CO_2$ levels as low as 1 to 1.5% by volume (Galantsev and Tumonov 1969). Also, lengthy exposure to low levels of $CO_2$ (2%) led to increased ventilation and decreased rectal temperatures in Merriam's kangaroo rats (*Dipodomys merriami*) (Soholt et al 1973). Withers (1975) working with small (20 gm.) semi-fossorial *Pseudomys albocinereus*, found a decreasing rectal temperature in response to all levels of $CO_2$ greater than ambient. Baudinette (1974) found the effect of $CO_2$ was greater when the animal was exposed to $CO_2$ outside thermoneutral temperatures of 20 to 30$^{o}$C. (Dawson 1955). The subnivean temperatures outside the nest (-7 to 0$^{o}$C.) are definitely outside the small mammals thermoneutral zone. Nests allow increases in temperatures from 7 to 24 C. greater than environmental conditions (Hayward 1965) but would also probably be areas of greater $CO_2$ concentrations because of occupation.

Therefore, small mammals can respond to increased concentrations of $CO_2$. Temperature or food are not necessarily correlated with changes in small mammal distribution. The response to increases in $CO_2$ concentrations may be related to changes in the distribution of small mammals.

# MATERIALS AND METHODS

## STUDY AREA

Field research was conducted around the Taiga Biological Station at 51°05' N lat.; 95° 20'W long. (Figure 1). The area is within the taiga or boreal coniferous forest on the Precambrian Shield. Habitats investigated were black spruce bog (Figure 2), aspen upland (Figure 3), alder tamarack bog (Figure 4), alder ridge ecotone (Figure 5), jackpine ridge (Figure 6), and jackpine sandplain (Figure 7).

Average precipitation is 50 to 60 cm. rainfall equivalent with 40 cm. falling as rain and the rest as snow (Atmospheric and Environmental Services 1970). Temperatures range from - 50 to +40°C with maximum temperatures in June and July and minima in January and February. The first major snowfall, establishing the hiemal threshold (snowcover thickness of 15 - 20 cm.), occurs in late November to early December, and snow disappears in late April or May.

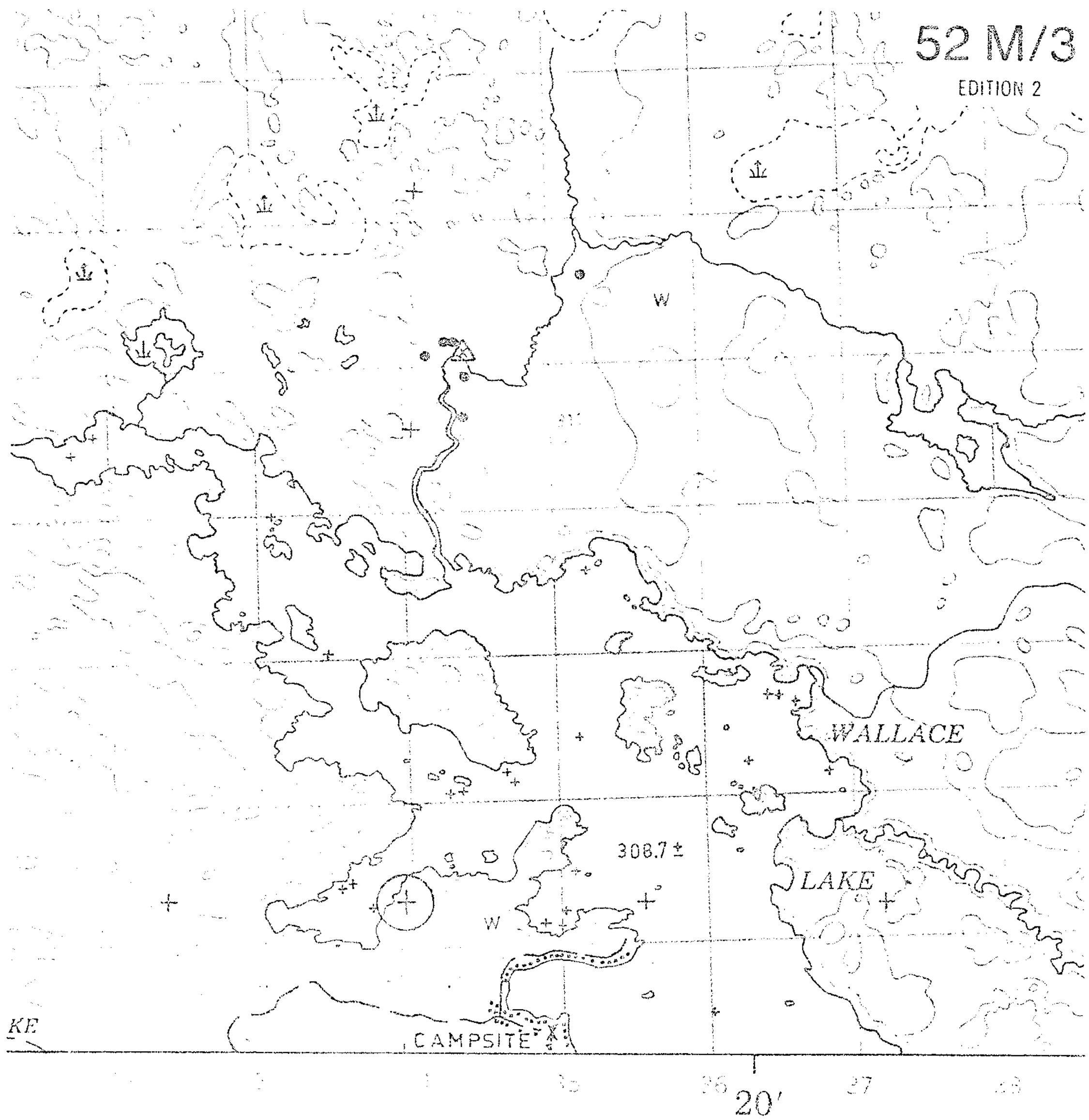
Square grids 0.4 ha. in size were established in each of the six habitat types. Each grid was composed of 100 small mammal trapping sites spaced equidistantly from each other in a 10 x 10 pattern

FIGURE 1

Map of the study area

△ Taiga Biological Station

● Study Plot




# AIKENS LAKE

## MANITOBA-ONTARIO

EAST OF PRINCIPAL MERIDIAN - EST DU MÉRIDIEN PRINCIPAL

Scale 1:50,000 Échelle

Miles 1 0 1 2 3 Miles

Metres 1000 0 1000 2000 3000 4000 Mètres

Yards 1000 0 1000 2000 3000 4000 Verges

FIGURE 2

Black spruce bog plot

FIGURE 3

Aspen upland plot

FIGURE 4

Alder tamarack bog plot

FIGURE 5

Alder ridge ecotone plot looking from
the ridge into the adjacent bog

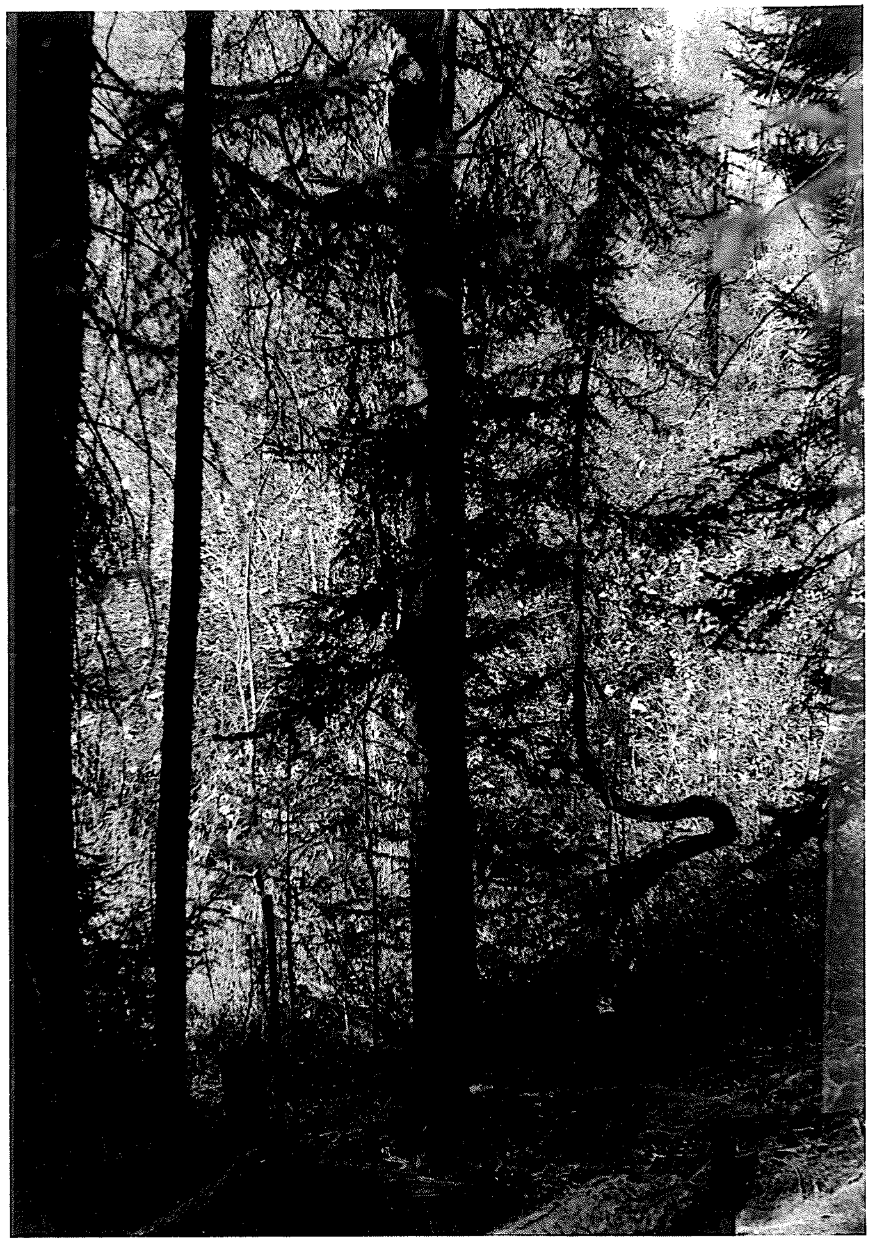
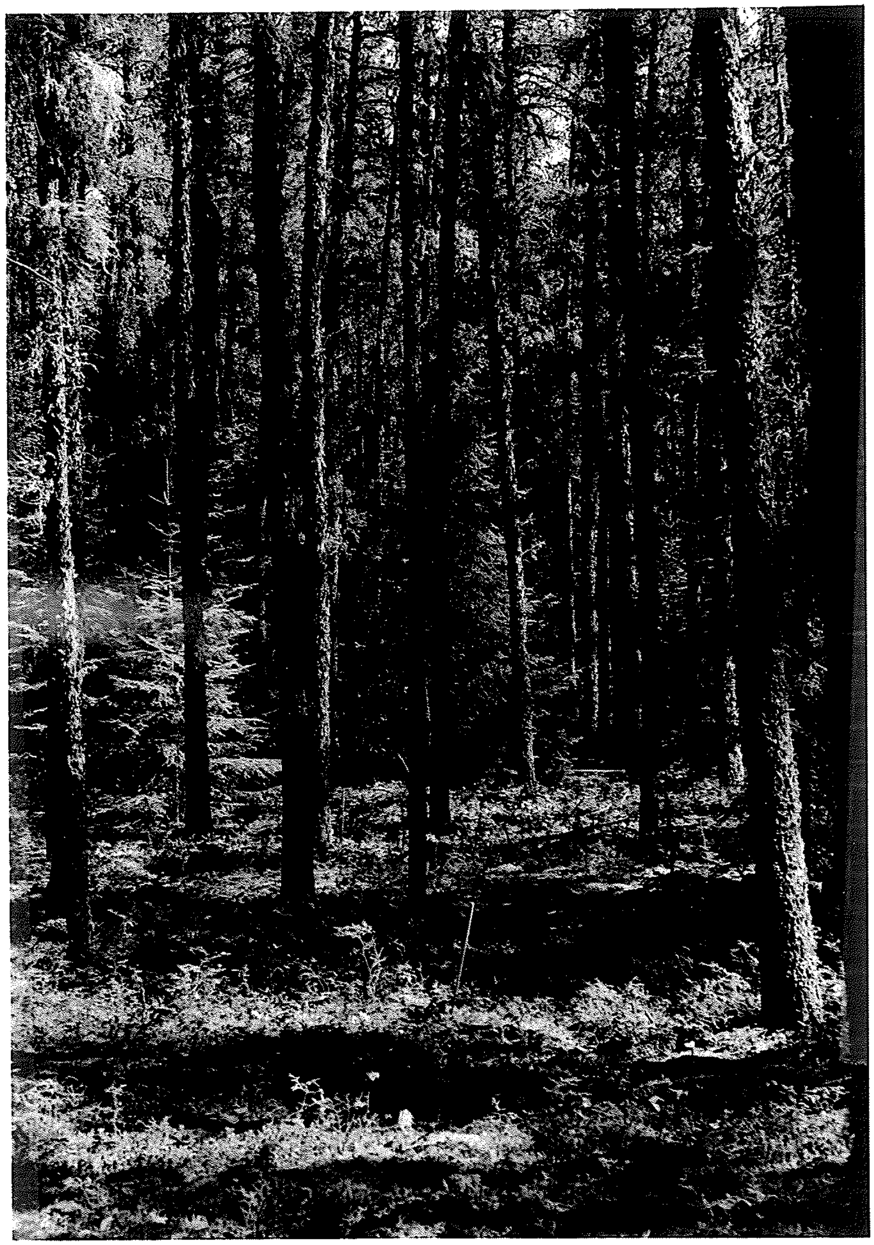


FIGURE 6

Jackpine ridge plot

FIGURE 7

Jackpine sandplain plot



each site about 6.5 m. apart. One axis of the grid was labelled A to J and the other axis was numbered 1 to 10. Each grid point was permanently marked by a wooden 2.5 cm. x 2.5 cm. x 1.5 m. stake with alternate yellow and black decimeter markings.

SECTION 1

## $CO_2$ SAMPLING SITES

The same trapping areas were sampled for $CO_2$ and small mammals. At each $CO_2$ sampling site a 2 m. piece of rubber tubing (0.6 cm. inside diameter) was taped to one of the wooden stakes of the grid. The upper end was taped to the wooden stake and the lower end lay on the ground-air interface away from the regular grid pathways. $CO_2$ testing sites were established to sample as much as possible of the microtopographical and habitat variation.

Each $CO_2$ measuring site was sampled once per month from mid December 1973 to early April 1974 unless it was plugged or otherwise inoperable. This inability to measure $CO_2$ at some sites led to missing data. One site was set up at each of the most elevated and at the most depressed sites of the grid in the aspen upland and jackpine ridge plots. Two adjacent stations were chosen in each of the relatively flat alder bog and black spruce bog plots.

The sites for 1974 to 1975 consisted of lines of sampling stations along a microtopographical gradient from the highest to the lowest points on the jackpine ridge (five stations), aspen upland (ten stations), alder ridge ecotone (ten stations) and black spurce bog (five stations). A line of 10 $CO_2$ testing stations was also established across the alder tamarack bog and included all the microtopographical variation in the plot. Two $CO_2$ stations were established, one in the open, the other in the more densely forested part of the jackpine sandplain. Additional stations in differing microhabitats were placed within the aspen plot so that all soil and vegetation types could be sampled. On the alder ridge ecotone additional testing sites were located on the ridge area of the plot. No extra readings were taken in the bog because the alder tamarack bog plot and the ecotone plot are adjacent for half of their length. All stations were tested at least three times a month from early December to mid April.

$CO_2$ testing sites for 1975 to 1976 were the same as those of 1974 to 1975 with the addition of two subterranean (10 cm. deep) testing stations (one each in the greater $CO_2$ and lesser $CO_2$ accumulation areas in thick soil as determined from 1974 to 1975 data) in the aspen plot and two in presumed mouse holes in the alder ridge ecotone. These stations were checked three times a month or more.

## $CO_2$ ANALYSIS

$CO_2$ concentrations were measured using a Dräger multigas analyzer and analyzing tubes with a range of 0.01 to 0.3 ±.005%/volume. The meter and tubes were calibrated against a gas chromatograph (see Appendix A). The multigas analyzer is essentially a small hand pump with a one-way valve. During the $CO_2$ measurement, a redox reaction takes place in the measuring tube, causing a white to purple color change. The procedure for utilizing the analyzer in the field is found in Appendix B.

One problem encountered during the readings was the shattering of the glass measuring tubes in the analyzer. The $CO_2$ analyzer was inoperative during January 1976 and caused the loss of a number of weeks of data before it could be replaced. $CO_2$ was usually measured once a week at each station from the onset of the hiemal threshold until the snowcover was no longer continous or the testing station was exposed.

$CO_2$ readings were taken at two stations from 24 March 1975 to 27 March 1975 in an attempt to see if any variation occurred on day to day measurements. Kelley et al. (1968) found the least daily variation to occur between 1000 and 1600 hours. On 28 March 1975 hourly $CO_2$ readings were taken from 1200 to 2000 (dark) and 0600 to 1000 29 March 1975 to note $CO_2$ variation. Since the color change was not readily discernable when read in the light of propane or kerosene lamps, no further readings were taken after dark.

SECTION 2

## ENVIRONMENTAL PARAMETERS

### MICROTOPOGRAPHY

Accurate data were collected to find microtopographical gradients within the plots. This was done by establishing line transects down the A to J plot lines and along the #1 baseline of the plots. I measured the distance to the ground from a levelled string every 50 cm. along the transect lines. These readings were later corrected to make the lowest point equal to 0 and thus the total microtopographic variation in the plot could be visualized. Maps showing major features such as bare rock, large drops between lines and depressions between lines were also made.

### CLIMATE

Temperature, precipitation, phase of the moon, wind speed, cloud cover and barometric pressure were recorded each day at TBS. Temperature readings were taken at 0800 hours and daily maxima were also recorded. Precipitation was recorded by the weather station in Bissett. Barometric pressure was recorded at about 1500 , often 0800 and the time of the temperature maximum each day at TBS.

## SNOW CONDITIONS

Snow profiles were taken twice monthly adjacent to rather than on each of the plots to decrease human disturbance, using the methods and instruments outlined in Klein et al. (1950). These measurements included snow thickness, number of snow layers, thickness of each layer, hardness ($g/cm^2$), density ($g/cm^3$), temperature of each snow layer, presence of ice layers, crystal type within each snow layer as well as any peculiarities noted in the profile.

In 1973 to 1974 snow thickness was measured adjacent to each station for each $CO_2$ reading throughout that testing. In 1974 to 1975 snow thickness was measured only in March and April at each station for each $CO_2$ reading. In 1975 to 1976 the number of ice layers present in the profile as well as snow thickness were measured at each station for each $CO_2$ reading taken from December to April.

## SUBNIVEAN TEMPERATURE

Thermistors installed at 12 $CO_2$ testing stations during the summer were used to measure subnivean temperatures in the winters of 1973 to 1974 and 1975 to 1976. The thermistors were read using Sanwa Electric Instrument Company type P-3 ohmmeter. Their accuracy was not consistent so that temperatures in 1975 to 1976 were measured by using an ordinary thermometer ($\pm$ 0.5$^{\circ}$C) in a protective metal case. These temperature readings were taken at least 50 cm. from the subnivean opening of the $CO_2$ testing tube. This allowed individual temperature readings to be taken at each $CO_2$ station for every $CO_2$ reading taken. If ice layers were encountered, a wire was used to make a hole and then the thermometer was inserted to the ground level. The hole made by the thermometer was filled in after each measurement.

## STATISTICAL ANALYSIS

To carry out the statistical analysis parameters were defined, numbered and entered as in Table 1. To test the effect of subnivean temperature on $CO_2$ concentration a Pearson correlation coefficient was determined for both winters of 1974 to 1976 using the Statistical Package for the Social Sciences (SPSS).

To test the relationship of snow hardness and snow density a Pearson correlation coefficient was determined for both winters of 1974 to 1976 using SPSS. The means, standard errors and ranges of subnivean temperature and snowcover thickness were listed for each of the six plots using the Condescriptive SPSS file.

A step-wise Discriminant analysis (from SPSS) was used to determine those environmental parameters which were most closely associated with $CO_2$. A classification of $CO_2$ concentrations into three ranges was used: less than ambient (less than 0.0175%), ambient (0.0175% to 0.025%) and above ambient (more than 0.025%). The means and standard deviations of each variable within each of these groups

TABLE 1

DEFINITION OF ENVIRONMENTAL PARAMETERS AS USED IN STATISTICAL ANALYSIS

$Y_1$: $CO_2$ station number where $Y_1$ to $Y_{10}$ represent the alder tamarack bog, $Y_{11}$ to $Y_{20}$ the alder ridge ecotone, $Y_{21}$ to $Y_{30}$ the aspen upland, $Y_{31}$ to $Y_{35}$ the black spruce bog, $Y_{36}$ to $Y_{40}$ the jackpine ridge and $Y_{41}$ to $Y_{42}$ the jackpine sandplain.

$Y_2$: the change in microtopography where 0 is flat, 1 shows that the difference in height on both sides of the stake is larger than 100 cm, 2 shows that the difference in height on both sides of the stake is less than 100 cm.

$Y_3$: thickness of soil measured in cm up to 1 m.

$Y_4$: the percent of green vegetation in the ground cover of a 0.25 m quadrat at each $CO_2$ testing station prior to the first snowfall (not measured in 1974 to 1975).

$Y_1$ to $Y_4$ are site dependent factors that are constant over time.

$Y_5$: the chronological sequence of $CO_2$ measurements 1 to 15 (1974 to 1975) and 1 to 11 (1975 to 1976).

$Y_6$: $CO_2$ in %/volume x $10^4$.

$Y_7$: snowcover thickness in cm.

$Y_8$: subnivean temperature in $^oC$.

$Y_9$: number of ice layers in the snow adjacent to the $CO_2$ station (not measured at all stations in 1974 to 1975).

$Y_{10}$: total number of hardness readings in $gm/cm^2$, measured every two weeks.

$Y_{11}$: total number of density readings in $g/cm^3$, measured every two weeks.

$Y_{12}$: range of snow temperature in the profile x 10, measured every two weeks.

$Y_{13}$: ambient air temperature in $^oC$.

$Y_{14}$: barometric pressure in mmHg.

$Y_{15}$: change in barometric pressure.

is shown for both winters. The differences between groups is explained by the analysis. The minimum F statistic (comparing variances) was determined by the Wilks Method for Discriminant analysis.

A step-wise Discriminant analysis was done separately on the data from the different winters. Analysis of $CO_2$ was first carried out against all parameters, then against site-dependent parameters, site-independent parameters, the snow parameters and separately against subnivean temperatures and two snow parameters measured at each site. Separate analysis was done against the snow parameters because they were only measured once every two weeks. This led to missing cases which SPSS deleted in a listwise fashion and thus decreased the numbers eligible to each other analysis. Analysis was performed with the day effect and then without it. There was at least a 10% decrease in predictive value (percentage of "grouped" variables correctly calssified by significant variables) in 1975 to 1976 in contrast to no effect in 1974 to 1975 when the day effect was removed. Therefore to make comparisons more realistic this day effect was removed before the two years were compared.

SECTION 3

## SMALL MAMMAL TRAPPING

Small mammals were live-trapped throughout the study and toeclipped for later recognition. Sherman traps were used for all summer trapping and one trap was set at each of the 100 stakes on each plot. Sherman traps were not used before May nor after September because of the potential heat loss from their metal sides and the corresponding increased small mammal mortality. Trapping grids were established in June, July and August 1973 and were live-trapped immediately after they were established. The black spruce bog, the alder tamarack bog, the aspen upland and the jackpine ridge were each trapped with three trap checks per day. In order to get a broader idea of the number of type of species present than three-night trapping periods allowed (Smith 1966), I trapped these plots for 11 days each.

Summer trapping was carried out from May to September of both 1974 and 1975. Plots in the alder ridge ecotone and jackpine sandplain were established and trapped in September 1974. A three-night trapping schedule was followed and the traps were put on the plots in the early afternoon (Gentry and Odum 1957). Trapping was discontinued during any period of cold or rainy weather to prevent trap deaths due to exposure.

Masonite or Jolly-Board traps were used for all the winter trapping. These wooden traps transferred less heat than metal Shermans and thus reduced trap mortality. Also they were smaller in size than the Shermans and the animal had a smaller volume to keep warm. Winter trapping was done using wooden trap chimneys (Pruitt

1959b).

In the winter of 1973 to 1974 trapping was carried out in the alder tamarack bog and the black spruce bog at trap chimneys at every second stake for one three-night period.

In the winter of 1974 to 1975 trapping was carried out once a month in the alder tamarack bog, the alder ridge ecotone, the black spruce bog and the aspen upland from December to April. A trap chimney was placed at every fourth stake giving 25 trap chimneys in each habitat. All chimneys were pre-baited with raw oatflakes at least two different times before trapping began in December. This was intended to induce small mammals to include trap chimneys in their food search pattern and thus open subnivean tunnels to them in the winter. Prior to the hiemal threshold trapping was not normally carried out because it disrupts the normal subnivean space formation. In 1974, however, trapping was started in December even though the threshold was not reached because at that time it was felt that the data being lost were worth more than the disruptions of the subnivean space. Initially traps were checked every four hours; however, this proved too arduous so traps then were checked every six hours.

In the winter of 1975 to 1976 trapping was again carried out in the alder tamarack bog, the alder ridge ecotone, the black spruce bog and the aspen upland from October to April. The original pattern of the 1974 to 1975 trap chimneys was retained with 10 new chimneys added to the alder tamarack bog and aspen upland habitats alternating A - J, #4 and #5 trap markers, five new chimneys were added to the black spruce bog at B10, D10, F10, H10 and J10, and five to the alder ridge ecotone at A4, C4, E4, G4 and I4.

During the winter of 1975 to 1976 extra bait was added to the traps and they were checked every eight hours. During this year there was no snow until December and the hiemal threshold was then quickly reached so that trapping was possible for all but a few weeks in December.

The bait used for small mammal trapping was a combination of peanut butter, rolled oats and occasionally chopped raisin. Weight, sex and species were recorded for each animal to determine population structure.

# RESULTS

## SECTION 1.

### $CO_2$ ACCUMULATION

Carbon dioxide accumulations were considered to be important to small mammals when subnivean $CO_2$ concentrations were greater than ambient levels for two or more consecutive weekly samplings. This meant that $CO_2$ had been greater than ambient for at least one week and not just a momentary increase. It is important to note that I consistently measured ambient $CO_2$ at TBS to be 0.02%/volume whereas other studies have reported 0.028-0.035%/volume $CO_2$ and that I used the former value to define ambient conditions.

$CO_2$ accumulated at five of seven $CO_2$ sampling stations on the four habitats in 1973 to 1974, 22 of 39 in the six habitats in 1974 to 1975, and 23 of 44 in the six habitats in 1975 to 1976. Accumulations were recorded primarily in December, March to April and February to March, respectively in the winters of 1973-74, 1974-75 and 1975-76 (Table 2). The proportion of $CO_2$ measurements within the concentration ranges differed between habitats, but was the same from year to year within a given habitat. This was especially true in the aspen upland, alder tamarack bog, alder ridge ecotone and jackpine ridge (Table 3). The black spruce bog and jackpine sandplain exhibited a greater variation in $CO_2$ measurements between the two later years (Table 3).

TABLE 2

Monthly totals of $CO_2$ samples (%/volume) for the winters of 1973-76.

| Plot and period | | <0.015 | 0.015-0.025 | 0.025-0.045 | 0.045-0.065 | >0.065 |
|---|---|---|---|---|---|---|
| | | . . Number of $CO_2$ measurements . . | | | | |
| Black spruce bog | | | | | | |
| 1973-74: | December | 0 | 1 | 0 | 0 | 1 |
| | January | 0 | 0 | 1 | 0 | 0 |
| | February | 0 | 0 | 1 | 0 | 0 |
| | March | 0 | 1 | 0 | 1 | 0 |
| | April | 0 | 0 | 1 | 0 | 0 |
| 1974-75: | December | 0 | 13 | 3 | 0 | 0 |
| | January | 0 | 14 | 1 | 0 | 0 |
| | February | 0 | 10 | 5 | 0 | 0 |
| | March | 0 | 12 | 8 | 0 | 0 |
| | April | 0 | 3 | 7 | 0 | 0 |
| 1975-76: | December | 4 | 4 | 0 | 0 | 0 |
| | January | 4 | 11 | 0 | 0 | 0 |
| | February | 0 | 4 | 10 | 1 | 0 |
| | March | 0 | 7 | 6 | 7 | 0 |
| | April | 0 | 0 | 3 | 0 | 0 |
| Aspen upland | | | | | | |
| 1973-74: | December | 0 | 0 | 0 | 0 | 2 |
| | January | 0 | 1 | 1 | 0 | 0 |
| | February | 0 | 0 | 1 | 1 | 0 |
| | March | 0 | 2 | 0 | 2 | 0 |
| | April | 0 | 0 | 2 | 0 | 0 |
| 1974-75: | December | 2 | 16 | 9 | 0 | 0 |
| | January | 1 | 14 | 11 | 1 | 0 |
| | February | 1 | 11 | 11 | 3 | 1 |
| | March | 1 | 12 | 16 | 3 | 0 |
| | April | 0 | 4 | 8 | 2 | 0 |
| 1975-76: | December | 3 | 9 | 1 | 0 | 0 |
| | January | 1 | 19 | 2 | 0 | 0 |
| | February | 0 | 11 | 14 | 4 | 1 |
| | March | 0 | 13 | 16 | 9 | 0 |
| (without soil) | | | | | | |

. . . continued

TABLE 2 (CONTINUED)

| Plot and period | <0.015 | 0.015–0.025 | 0.025–0.045 | 0.045–0.065 | >0.065 |
|---|---|---|---|---|---|
| | . . Number of $CO_2$ measurements . . | | | | |
| Alder tamarack bog | | | | | |
| 1973-74: December | 2 | 0 | 3 | 0 | 0 |
| January | 0 | 1 | 1 | 0 | 0 |
| February | 0 | 2 | 0 | 0 | 0 |
| March | 1 | 3 | 0 | 0 | 0 |
| April | 0 | 2 | 0 | 0 | 0 |
| 1974-75: December | 0 | 24 | 3 | 0 | 0 |
| January | 2 | 24 | 1 | 0 | 0 |
| February | 2 | 22 | 3 | 0 | 0 |
| March | 1 | 19 | 7 | 0 | 0 |
| April | 2 | 21 | 5 | 0 | 0 |
| 1975-76: December | 5 | 5 | 0 | 0 | 0 |
| January | 0 | 23 | 0 | 0 | 0 |
| February | 0 | 36 | 1 | 0 | 0 |
| March | 0 | 21 | 9 | 0 | 0 |
| Alder ridge ecotone | | | | | |
| 1974-75: December | 0 | 20 | 5 | 0 | 0 |
| January | 3 | 18 | 4 | 0 | 0 |
| February | 3 | 19 | 5 | 0 | 0 |
| March | 0 | 19 | 7 | 0 | 0 |
| April | 1 | 14 | 6 | 2 | 0 |
| 1975-76: December | 5 | 5 | 0 | 0 | 0 |
| January | 3 | 19 | 3 | 0 | 0 |
| February | 0 | 23 | 7 | 0 | 0 |
| March | 0 | 26 | 10 | 3 | 0 |
| Jackpine ridge | | | | | |
| 1973-74: December | 0 | 2 | 0 | 0 | 0 |
| January | 0 | 2 | 0 | 0 | 0 |
| February | 0 | 1 | 1 | 0 | 0 |
| March | 0 | 2 | 1 | 0 | 0 |
| April | 0 | 2 | 0 | 0 | 0 |

. . . continued

TABLE 2 (CONTINUED)

| Plot and period | <0.015 | 0.015–0.025 | 0.025–0.045 | 0.045–0.065 | >0.065 |
|---|---|---|---|---|---|
| | . . Number of $CO_2$ measurements . . | | | | |
| Jackpine ridge (continued) | | | | | |
| 1974-75: December | 0 | 9 | 0 | 0 | 0 |
| January | 1 | 10 | 1 | 0 | 0 |
| February | 0 | 9 | 1 | 0 | 0 |
| March | 0 | 18 | 2 | 0 | 0 |
| April | 0 | 8 | 0 | 0 | 0 |
| 1975-76: December | 0 | 5 | 0 | 0 | 0 |
| January | 1 | 13 | 1 | 0 | 0 |
| February | 1 | 12 | 2 | 0 | 0 |
| March | 0 | 13 | 2 | 0 | 0 |
| April | 0 | 0 | 3 | 0 | 0 |
| Jackpine sandplain | | | | | |
| 1974-75: December | 0 | 6 | 0 | 0 | 0 |
| January | 0 | 5 | 1 | 0 | 0 |
| February | 0 | 3 | 1 | 0 | 0 |
| March | 1 | 5 | 2 | 0 | 0 |
| April | 0 | 4 | 0 | 0 | 0 |
| 1975-76: December | 0 | 2 | 0 | 0 | 0 |
| January | 1 | 4 | 1 | 0 | 0 |
| February | 0 | 3 | 3 | 0 | 0 |
| March | 0 | 4 | 2 | 0 | 2 |

TABLE 3

Measured $CO_2$ concentrations (%/volume) and accumulations from six habitats during winters 1973-74, 1974-75 and 1975-76.

| Plot and period | < 0.015 | | 0.015-0.025 | | 0.025-0.045 | | 0.045-0.065 | | > 0.065 | | Total no. of readings | No. of stations with accumulation | No. of stations without accumulation |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $CO_2$ concentrations (%/volume) | | | | | | | | | | | | |
| | No. | % | No. | % | No. | % | No. | % | No. | % | | | |
| Black spruce bog | | | | | | | | | | | | | |
| 1973-74 | 0 | 0 | 2 | 29 | 3 | 43 | 1 | 14 | 1 | 14 | 7 | 1 | 0 |
| 1974-75 | 0 | 0 | 52 | 68 | 24 | 32 | 0 | 0 | 0 | 0 | 76 | 3 | 2 |
| 1975-76 | 8 | 13 | 26 | 43 | 19 | 31 | 8 | 13 | 0 | 0 | 61 | 5 | 0 |
| Aspen | | | | | | | | | | | | | |
| 1973-74 | 0 | 0 | 3 | 25 | 4 | 33 | 3 | 25 | 2 | 17 | 12 | 2 | 0 |
| 1974-75 | 5 | 4 | 57 | 45 | 55 | 43 | 9 | 7 | 1 | 1 | 127 | 8 | 1 |
| 1975-76* | 4 | 3 | 59 | 47 | 37 | 30 | 15 | 12 | 10 | 8 | 125 | 11 | 1 |
| 1975-75** | 4 | 4 | 52 | 50 | 33 | 32 | 13 | 13 | 1 | 1 | 103 | 9 | 1 |
| 1975-76*** | 4 | 4 | 45 | 49 | 29 | 32 | 12 | 13 | 1 | 1 | 91 | 8 | 1 |
| Alder tamarack bog | | | | | | | | | | | | | |
| 1973-74 | 3 | 20 | 8 | 53 | 4 | 27 | 0 | 0 | 0 | 0 | 15 | 1 | 1 |
| 1974-75 | 7 | 5 | 110 | 81 | 19 | 14 | 0 | 0 | 0 | 0 | 136 | 3 | 6 |
| 1975-76 | 5 | 5 | 85 | 85 | 10 | 10 | 0 | 0 | 0 | 0 | 100 | 0 | 10 |
| Alder ridge ecotone | | | | | | | | | | | | | |
| 1974-75 | 7 | 6 | 90 | 71 | 27 | 21 | 2 | 2 | 0 | 0 | 126 | 7 | 2 |
| 1975-76 | 8 | 8 | 73 | 70 | 20 | 19 | 3 | 3 | 0 | 0 | 104 | 4 | 6 |
| Jackpine ridge | | | | | | | | | | | | | |
| 1973-74 | 0 | 0 | 9 | 82 | 2 | 18 | 0 | 0 | 0 | 0 | 11 | 1 | 1 |
| 1974-75 | 1 | 2 | 54 | 92 | 4 | 7 | 0 | 0 | 0 | 0 | 59 | 0 | 5 |
| 1975-76 | 2 | 4 | 43 | 81 | 8 | 15 | 0 | 0 | 0 | 0 | 53 | 1 | 4 |
| Jackpine sandplain | | | | | | | | | | | | | |
| 1974-75 | 1 | 4 | 23 | 82 | 4 | 14 | 0 | 0 | 0 | 0 | 28 | 1 | 1 |
| 1975-76 | 1 | 5 | 13 | 59 | 6 | 27 | 0 | 0 | 2 | 9 | 22 | 2 | 0 |

*With soil
**Without soil
***Without A6 and soil

The 1973 to 1974 $CO_2$ sampling stations were used as a pilot study to determine the location and number of sites to be used in the following two winters. Comparison between winter 1973 to 1974 and those of 1974 to 1975 and 1975 to 1976 was not emphasized because of the small sample size in 1973 to 1974 (only two sampling stations/ plot and both those were not always in operation for the monthly samplings). The winter of 1973 to 1974 was also different in that the maximum snowcover thickness was double that found during the other two winters.

The aspen upland exhibited a progressive increase in $CO_2$ concentrations (Table 2). The same progressive increase can be seen in both years in the alder ridge ecotone, but the maximum $CO_2$ concentrations were less. The black spruce bog exhibited this increase in concentration in the winter 1975 to 1976. The jackpine sandplain showed a less pronounced but still evident increase in concentrations in 1975 to 1976.

In neither the alder tamarack bog nor jackpine ridge did $CO_2$ concentrations show an increase as the year progressed nor was there any obvious accumulation of $CO_2$ during the year (Table 2). The black spruce bog and jackpine sandplain did not show marked $CO_2$ increases in the winter 1974 to 1975.

$CO_2$ measurements taken in the soil at two stations in the aspen upland habitat were always equal to or greater than adjacent measurements taken at the soil-snow interface (Table 4).

$CO_2$ measurements taken within the snow profile were found to be consistent within the measurable variation of the $CO_2$ meter, except on 12 January 1974 when the range was from 0.0175 to 0.03%/volume $CO_2$ (Table 5).

$CO_2$ measurements taken hourly from 1200 to 2000 March 28, and 0600 to 1000 29 March, 1975 ranged from 0.01 to 0.02%/volume which I considered to be insignificant (Table 6). Daily measurements taken at the same stake and same time of day from 24 to 27 March 1975 were found to be consistent at 0.0175 to 0.02%/volume $CO_2$.

$CO_2$ measurements of the air in two mouse holes were found to be less than or equal to ambient and were discontinued after two months because no occupation was evident.

SECTION 2.

## FACTORS INFLUENCING $CO_2$ ACCUMULATION

The overall ability of a model based on environmental parameters to predict the $CO_2$ concentrations in 1974 to 1975 was slightly less than half that in 1975 to 1976 (38.6%, 61.3%) (Table 7 and 8). The lack of consistency between the predictive values of the two winters may be due to the variability of different lag effects of time on $CO_2$

TABLE 4

Table of $CO_2$ concentrations (%/volume) in soil (10 cm. below surface) and adjacent $CO_2$ testing tubes in aspen plot taken once on each date in 1975-76

| | December 1975 | | January 1976 | | February 1976 | | | | March 1976 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 15 | 23 | 10 | 16 | 2 | 9 | 14 | 24 | 4 | 13 | 19 | 31 |
| Station C7 | | | | | | | | | | | | |
| Subnivean | | 0.0175-0.02 | inoperative meter | 0.015-0.0175 | 0.04-0.045 | 0.04-0.045 | 0.04 | 0.055-0.06 | 0.035-0.04 | 0.035-0.04 | 0.06 | 0.04 |
| Soil | | 0.025 | | 0.04 | 0.06-0.065 | 0.07-0.075 | 0.06-0.07 | 0.10-0.11 | 0.08 | 0.07-0.075 | | |
| Station F4 | | | | | | | | | | | | |
| Subnivean | 0.01-0.015 | 0.01-0.015 | | 0.01-0.015 | 0.0175-0.02 | 0.02-0.025 | 0.035-0.04 | 0.04 | 0.02 | 0.02 | 0.04 | 0.02 |
| Soil | 0.02 | 0.015-0.0175 | | 0.015-0.0175 | 0.02 | 0.02-0.025 | 0.04-0.045 | 0.04 | 0.02-0.025 | 0.02-0.025 | 0.05-0.06 | 0.08 |

TABLE 5

$CO_2$ concentrations (%/volume) measured once on each date within the snow profile at the ground-snow interface, 20 cm. above the ground and 40 cm. above the ground in the alder tamarack bog at station 17

| Date of Measurement | Subnivean $CO_2$ | 20 cm above ground $CO_2$ | 40 cm above ground $CO_2$ |
|---|---|---|---|
| 19 December 1973 | 0.0100 | 0.0125 | 0.0125 |
| 27 December 1973 | 0.0375-0.0400 | 0.0375-0.0400 | 0.0375-0.0400 |
| 12 January 1974 | 0.0200-0.0250 | 0.0175-0.0200 | 0.0250-0.0300 |
| 23 February 1974 | * | 0.0200-0.0250 | 0.0200-0.0250 |
| 17 March 1974 | 0.0200-0.0250 | 0.0200-0.0250 | 0.0200-0.0250 |
| 7 April 1974 | 0.0175-0.0200 | 0.0175-0.0200 | 0.0175-0.0200 |

*Blocked.

TABLE 6

Hourly sampling of subnivean $CO_2$ (%/volume) concentrations at two stations on 28 and 29 March 1975

| Date and time | Station #1 | Station #2 |
|---|---|---|
| 28 March: 1200 | 0.0175-0.02 | 0.02 |
| 1300 | 0.010-0.015 | 0.0175-0.02 |
| 1400 | 0.0175-0.02 | 0.02 |
| 1500 | 0.015-0.0175 | 0.02 |
| 1600 | 0.0175-0.02 | 0.02 |
| 1700 | 0.015-0.0175 | 0.0175-0.02 |
| 1800 | 0.0175-0.02 | 0.02 |
| 1900 | -- | 0.02 |
| 2000 | 0.02 | 0.02 |
| 2100 - 0600 not enough daylight to continue readings. | | |
| 29 March: 0600 | 0.01-0.015 | 0.0175-0.02 |
| 0700 | 0.015-0.0175 | 0.02 |
| 0800 | 0.015-0.0175 | 0.02 |
| 0900 | 0.0175-0.02 | 0.02 |
| 1000 | 0.0175-0.02 | 0.02 |

TABLE 7

Discriminant analysis of winter 1974-75 site-dependent and site-independent environmental factors with grouped $CO_2$

| Analysis | No. of cases | First 3 significant variables | | | Percent of "grouped" variables correctly classified by significant variables |
|---|---|---|---|---|---|
| With $Y_5$: $Y_6$ vs. $Y_2$, $Y_3$, $Y_5$, $Y_7$-$Y_{15}$ | 585 | $Y_7$ | $Y_{14}$ | $Y_3$ | 38.63 |
| $Y_6$ vs. $Y_2$, $Y_3$, $Y_5$ | 585 | $Y_3$ | - | - | 20.00 |
| $Y_6$ vs. $Y_7$-$Y_9$, $Y_{13}$-$Y_{15}$ | 585 | $Y_7$ | $Y_{14}$ | $Y_{13}$ | 36.41 |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 585 | $Y_{12}$ | $Y_{11}$ | $Y_{10}$ | 50.77 |
| Without $Y_5$: $Y_6$ vs. $Y_2$, $Y_3$, $Y_5$, $Y_7$-$Y_{15}$ | 585 | $Y_7$ | $Y_{14}$ | $Y_3$ | 40.00 |
| $Y_6$ vs. $Y_2$, $Y_3$, $Y_5$ | 585 | $Y_3$ | - | - | 20.00 |
| $Y_6$ vs. $Y_7$-$Y_9$, $Y_{13}$-$Y_{15}$ | 585 | $Y_7$ | $Y_{14}$ | $Y_{13}$ | 36.41 |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 585 | $Y_{12}$ | $Y_{11}$ | $Y_{10}$ | 50.77 |
| Alder tamarack bog (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$, $Y_3$, $Y_7$-$Y_{15}$ | 135 | $Y_7$ | $Y_{12}$ | $Y_{13}$ | 40.74 |
| $Y_6$ vs. $Y_2$, $Y_3$ | 135 | - | - | - | |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 135 | - | - | - | |
| $Y_6$ vs. $Y_7$-$Y_9$ | 135 | $Y_7$ | | - | 31.85 |
| Alder ridge ecotone (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$, $Y_3$, $Y_7$-$Y_{15}$ | 135 | $Y_{10}$ | $Y_9$ | $Y_2$ | 42.96 |
| $Y_6$ vs. $Y_2$, $Y_3$ | 135 | - | - | - | |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 135 | $Y_{10}$ | $Y_{11}$ | $Y_{12}$ | 31.85 |
| $Y_6$ vs. $Y_7$-$Y_9$ | 135 | $Y_7$ | $Y_9$ | - | 39.26 |
| Aspen upland (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$, $Y_3$, $Y_7$-$Y_{15}$ | 135 | $Y_3$ | $Y_{10}$ | $Y_7$ | 25.19 |
| $Y_6$ vs. $Y_2$, $Y_3$ | 135 | $Y_3$ | - | - | 39.26 |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 135 | $Y_{10}$ | - | - | * |
| $Y_6$ vs. $Y_7$-$Y_9$ | 135 | $Y_8$ | $Y_7$ | - | 45.93 |
| Black spruce bog (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$, $Y_3$, $Y_7$-$Y_{15}$ | 71 | $Y_{14}$ | $Y_{13}$ | $Y_{15}$ | 74.65 |
| $Y_6$ vs. $Y_2$, $Y_3$ | 71 | - | - | - | |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 71 | $Y_{12}$ | $Y_{11}$ | - | 66.20 |
| $Y_6$ vs. $Y_7$-$Y_9$ | 71 | - | - | - | |
| Jackpine ridge (without $Y_5$)** | | | | | |
| $Y_6$ vs. $Y_2$, $Y_3$, $Y_7$-$Y_{15}$ | 70 | $Y_{13}$ | $Y_7$ | $Y_{12}$ | 71.43 |
| $Y_6$ vs. $Y_2$, $Y_3$ | 70 | - | - | - | |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 70 | $Y_{10}$ | - | - | * |
| $Y_6$ vs. $Y_7$-$Y_9$ | 70 | - | - | - | |
| Jackpine sandplain (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$, $Y_3$, $Y_7$-$Y_{15}$ | | - | - | - | |
| $Y_6$ vs. $Y_2$, $Y_3$*** | | - | - | - | |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | | - | - | - | |
| $Y_6$ vs. $Y_7$-$Y_9$ | | - | - | - | |

*Reduced space dispersion matrix cannot be inverted.
**Groups 1 and 2 only.
***Groups 2 and 3 only.

TABLE 8

Discriminant analysis of winter 1975-76 site-dependent and site-independent environmental factors with grouped $CO_2$

| Analysis | No. of cases | First 3 significant variables | | | Percent of "grouped" variables correctly classified by significant variables |
|---|---|---|---|---|---|
| With $Y_5$: $Y_6$ vs. $Y_2$-$Y_5$, $Y_7$-$Y_{15}$ | 462 | $Y_5$ | $Y_{14}$ | $Y_{12}$ | 61.26 |
| $Y_6$ vs. $Y_2$-$Y_5$ | 462 | $Y_5$ | $Y_2$ | $Y_3$ | 53.38 |
| $Y_6$ vs. $Y_7$-$Y_9$, $Y_{13}$-$Y_{15}$ | 462 | $Y_{14}$ | $Y_9$ | $Y_{15}$ | 47.40 |
| Without $Y_5$: $Y_6$ vs. $Y_2$-$Y_4$, $Y_7$-$Y_{15}$ | 462 | $Y_{11}$ | $Y_{14}$ | $Y_7$ | 51.08 |
| $Y_6$ vs. $Y_2$-$Y_4$ | 462 | $Y_2$ | - | - | 21.43 |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 462 | $Y_{11}$ | $Y_{12}$ | $Y_{10}$ | 60.17 |
| Alde' tamarack bog (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$-$Y_4$, $Y_7$-$Y_{15}$* | 100 | $Y_7$ | $Y_{15}$ | $Y_{13}$ | 69.00 |
| $Y_6$ vs. $Y_2$-$Y_4$ | 100 | - | - | - | |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 100 | $Y_{11}$ | $Y_{10}$ | - | 69.00 |
| $Y_6$ vs. $Y_7$-$Y_9$ | 100 | $Y_7$ | - | - | 18.00 |
| Alder ridge ecotone (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$-$Y_4$, $Y_7$-$Y_{15}$ | 110 | $Y_{11}$ | $Y_{14}$ | $Y_4$ | 35.43 |
| $Y_6$ vs. $Y_2$-$Y_4$ | 110 | $Y_4$ | $Y_3$ | $Y_2$ | 45.45 |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 110 | $Y_{11}$ | $Y_{10}$ | - | 51.82 |
| $Y_6$ vs. $Y_7$-$Y_9$ | 110 | $Y_8$ | $Y_9$ | - | 47.27 |
| Aspen upland (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$-$Y_4$, $Y_7$-$Y_{15}$ | 110 | $Y_{11}$ | $Y_{13}$ | $Y_7$ | 64.55 |
| $Y_6$ vs. $Y_2$-$Y_4$ | 110 | $Y_3$ | $Y_2$ | - | 43.64 |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 110 | $Y_{11}$ | $Y_{12}$ | $Y_{10}$ | 54.55 |
| $Y_6$ vs. $Y_7$-$Y_9$ | 110 | $Y_7$ | $Y_8$ | - | 56.36 |
| Black spruce bog (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$-$Y_4$, $Y_7$-$Y_{15}$ | 55 | $Y_8$ | $Y_9$ | $Y_7$ | 54.55 |
| $Y_6$ vs. $Y_2$-$Y_4$ | 55 | - | - | - | |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 55 | $Y_{11}$ | $Y_{10}$ | $Y_{12}$ | 56.36 |
| $Y_6$ vs. $Y_7$-$Y_9$ | 55 | $Y_8$ | $Y_9$ | $Y_7$ | 78.18 |
| Jackpine ridge (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$-$Y_4$, $Y_7$-$Y_{15}$** | 49 | $Y_3$ | $Y_{14}$ | - | 73.47 |
| $Y_6$ vs. $Y_2$-$Y_4$ | 49 | $Y_3$ | - | - | 61.22 |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 49 | - | - | - | |
| $Y_6$ vs. $Y_7$-$Y_9$ | 49 | $Y_7$ | $Y_9$ | $Y_8$ | 46.94 |
| Jackpine sandplain (without $Y_5$) | | | | | |
| $Y_6$ vs. $Y_2$-$Y_4$, $Y_7$-$Y_{15}$** | 19 | $Y_7$ | $Y_9$ | $Y_4$ | 78.95 |
| $Y_6$ vs. $Y_2$-$Y_4$ | 19 | - | - | - | |
| $Y_6$ vs. $Y_{10}$-$Y_{12}$ | 19 | - | - | - | |
| $Y_6$ vs. $Y_7$-$Y_9$ | 19 | $Y_7$ | $Y_9$ | - | 78.95 |

*Groups 1 and 2 only.
**Groups 2 and 3 only.

accumulation. The same parameters reacted differently in different winters. This might lead to lower predictive values, especially when many parameters are closely related and their effects cannot be disassociated from one another (Table 9 and 10). A 30% predictive value is expected from random distribution so that 60% predictive value is significant given the time lag associated between the measured variables and their effects on $CO_2$ production and accumulation (Neil Arnason, personal communication). The largest predictive values were found in the black spruce bog and jackpine ridge in 1974 to 1975 and the jackpine ridge and jackpine sandplain in 1975 to 1976. However, in both years these plots had the fewest number of cases of the six plots. In 1974 to 1975 the day effect was closely associated with the number of ice layers, snow hardness, density and ambient air temperature, which are themselves interrelated. In 1975 to 1976 the only strong association is seen between the day effect and snow density, with a lesser association between the day effect and number of ice layers in the snow profile.

To get a more accurate idea of what was associated with $CO_2$ accumulation the day effect was removed. Then, in the analysis where all parameters except date were analyzed against $CO_2$, snow characteristics were found to be of first significance in the alder tamarack bog (snowcover thickness) and the alder ridge ecotone (snow hardness) in 1974 and 1975, and in the alder tamarack bog (snowcover thickness), alder ridge ecotone (snow density), aspen upland (snow density) and jackpine sandplain (snowcover thickness) in 1975 to

TABLE 9A

Means, standard deviations and F ratios of all environmental parameters in three different $CO_2$ groups for winter 1975-76

| | $Y_2$ | $Y_3$ | $Y_4$ | $Y_5$ | $Y_7$ | $Y_8$ | $Y_9$ | $Y_{10}$ | $Y_{11}$ | $Y_{12}$ | $Y_{13}$ | $Y_{14}$ | $Y_{15}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Group 1* | | | | | | | | | | | | | |
| $\bar{X}$ | 3.6970 | 3.3939 | 2.6970 | 1.6364 | 24.6060 | -70.9091 | 0.0000 | 13.6364 | 152.3636 | 29.6970 | -122.1212 | 2,973.3938 | 1.3030 |
| SD | 0.6386 | 1.8361 | 1.2371 | 0.9293 | 7.3184 | 27.2275 | 0.0000 | 5.6282 | 13.2338 | 21.9353 | 93.3661 | 13.2665 | 0.4667 |
| Group 2** | | | | | | | | | | | | | |
| $\bar{X}$ | 3.4384 | 3.3151 | 2.4452 | 5.4589 | 33.7123 | -49.8630 | 0.4658 | 331.3354 | 195.3904 | 37.7877 | -137.3972 | 2,967.4041 | 1.5479 |
| SD | 1.0568 | 1.8672 | 1.2207 | 2.8506 | 10.7979 | 27.7982 | 0.6233 | 751.6003 | 37.7193 | 21.4965 | 90.1039 | 15.2659 | 0.5763 |
| Group 3*** | | | | | | | | | | | | | |
| $\bar{X}$ | 3.0444 | 3.5556 | 2.3778 | 7.7333 | 37.0444 | -26.5555 | 0.5778 | 309.0000 | 227.9556 | 24.7778 | -50.0000 | 2,943.7554 | 1.9556 |
| SD | 1.2424 | 1.7781 | 1.4815 | 2.4346 | 10.7004 | 30.0874 | 0.4995 | 830.8787 | 45.7451 | 24.6096 | 85.3602 | 29.9333 | 0.5623 |
| F ratio | 4.0100 | 0.2941 | 0.6638 | 53.6762 | 14.6424 | 21.8578 | 11.8977 | 2.7200 | 39.5533 | 6.6197 | 16.3898 | 34.0000 | 14.3814 |

*Group 1: <0.015%/volume $CO_2$
**Group 2: 0.015-0.025%/volume $CO_2$
***Group 3: >0.025%/volume $CO_2$

TABLE 9B

Within groups correlation matrix of all environmental parameters except $CO_2$ for 1975-76

| | $Y_2$ | $Y_3$ | $Y_4$ | $Y_5$ | $Y_7$ | $Y_8$ | $Y_9$ | $Y_{10}$ | $Y_{11}$ | $Y_{12}$ | $Y_{13}$ | $Y_{14}$ | $Y_{15}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $Y_2$ | 1.0000 | | | | | | | | | | | | |
| $Y_3$ | 0.2238 | 1.0000 | | | | | | | | | | | |
| $Y_4$ | 0.2859 | 0.2780 | 1.0000 | | | | | | | | | | |
| $Y_5$ | 0.0830 | -0.1339 | 0.1196 | 1.0000 | | | | | | | | | |
| $Y_7$ | -0.0687 | 0.2558 | 0.0250 | 0.1815 | 1.0000 | | | | | | | | |
| $Y_8$ | -0.0246 | 0.0500 | -0.1290 | 0.3157 | 0.1781 | 1.0000 | | | | | | | |
| $Y_9$ | 0.0707 | -0.0661 | 0.0122 | 0.6484 | 0.1057 | 0.1885 | 1.0000 | | | | | | |
| $Y_{10}$ | 0.1384 | 0.1707 | 0.2392 | 0.3508 | 0.0335 | 0.1200 | 0.4884 | 1.0000 | | | | | |
| $Y_{11}$ | 0.0570 | -0.0865 | 0.0771 | 0.8739 | 0.1108 | 0.4690 | 0.4688 | 0.2125 | 1.0000 | | | | |
| $Y_{12}$ | -0.0119 | 0.2266 | -0.0789 | -0.1283 | 0.2045 | -0.3227 | -0.0080 | -0.0354 | -0.2006 | 1.0000 | | | |
| $Y_{13}$ | -0.1111 | -0.1620 | -0.1184 | 0.0811 | -0.1043 | 0.2529 | -0.0189 | -0.0994 | 0.2514 | -0.2275 | 1.0000 | | |
| $Y_{14}$ | 0.0469 | 0.1501 | 0.1093 | 0.0115 | 0.0280 | -0.4429 | 0.2932 | 0.3896 | -0.2114 | 0.3479 | -0.4994 | 1.0000 | |
| $Y_{15}$ | -0.0305 | -0.0528 | 0.0454 | 0.0861 | 0.1417 | 0.1246 | -0.0896 | -0.3395 | 0.0369 | 0.0818 | 0.2224 | -0.0497 | 1.0000 |

TABLE 10A

Means, standard deviations and F ratios of all environmental parameters in three different $CO_2$ groups for winter 1974-75

| | $Y_2$ | $Y_3$ | $Y_5$ | $Y_7$ | $Y_8$ | $Y_9$ | $Y_{10}$ | $Y_{11}$ | $Y_{12}$ | $Y_{13}$ | $Y_{14}$ | $Y_{15}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Group 1* | | | | | | | | | | | | |
| $\bar{X}$ | 3.5333 | 3.0000 | 8.9333 | 38.2000 | -56.6667 | 0.4000 | 221.8000 | 231.2000 | 20.0000 | -118.0000 | 2,957.1333 | 1.6000 |
| SD | 1.0601 | 1.9640 | 4.0614 | 10.2901 | 19.3342 | 0.5071 | 387.2166 | 53.6646 | 11.0195 | 106.5833 | 36.9401 | 0.7368 |
| Group 2** | | | | | | | | | | | | |
| $\bar{X}$ | 3.6066 | 3.0328 | 9.5574 | 38.8524 | -52.0492 | 0.5246 | 243.6721 | 239.0164 | 25.2623 | -93.5246 | 2,966.8032 | 1.7377 |
| SD | 0.9179 | 1.9146 | 3.3542 | 13.0203 | 17.9670 | 0.5035 | 403.9604 | 62.9431 | 17.8987 | 92.0614 | 20.6559 | 0.7938 |
| Group 3*** | | | | | | | | | | | | |
| $\bar{X}$ | 3.4375 | 3.8750 | 10.3750 | 30.1250 | -43.7500 | 0.5625 | 439.3125 | 241.3750 | 17.8125 | -32.8125 | 2,976.2500 | 2.0625 |
| SD | 1.2093 | 1.7464 | 4.2564 | 12.1758 | 23.6291 | 0.5123 | 641.7971 | 71.0069 | 17.0263 | 128.5557 | 20.4222 | 0.9287 |
| F ratio | 0.1920 | 1.3270 | 0.6193 | 3.1502 | 1.8597 | 0.4666 | 1.3157 | 0.1183 | 1.5438 | 3.1107 | 3.1102 | 1.4232 |

*Group 1: <0.015%/volume $CO_2$
**Group 2: 0.015-0.025%/volume $CO_2$
***Group 3: >0.025%/volume $CO_2$

TABLE 10B

Within groups correlation matrix of all environmental parameters except $CO_2$ for 1974-75

| | $Y_2$ | $Y_3$ | $Y_5$ | $Y_7$ | $Y_8$ | $Y_9$ | $Y_{10}$ | $Y_{11}$ | $Y_{12}$ | $Y_{13}$ | $Y_{14}$ | $Y_{15}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $Y_2$ | 1.0000 | | | | | | | | | | | |
| $Y_3$ | 0.1707 | 1.0000 | | | | | | | | | | |
| $Y_5$ | 0.1498 | -0.0234 | 1.0000 | | | | | | | | | |
| $Y_7$ | -0.0533 | 0.1830 | -0.1562 | 1.0000 | | | | | | | | |
| $Y_8$ | -0.2020 | -0.3537 | 0.3707 | -0.3317 | 1.0000 | | | | | | | |
| $Y_9$ | 0.0547 | -0.1750 | 0.8625 | -0.1452 | 0.3571 | 1.0000 | | | | | | |
| $Y_{10}$ | 0.1884 | -0.0437 | 0.7142 | -0.4876 | 0.4343 | 0.5419 | 1.0000 | | | | | |
| $Y_{11}$ | 0.1413 | -0.0280 | 0.8244 | -0.3614 | 0.3665 | 0.7008 | 0.7459 | 1.0000 | | | | |
| $Y_{12}$ | 0.0192 | 0.3089 | -0.5215 | 0.4172 | -0.4816 | -0.4731 | -0.4805 | -0.6133 | 1.0000 | | | |
| $Y_{13}$ | 0.1507 | -0.0885 | 0.8244 | -0.3786 | 0.4673 | 0.6784 | 0.7421 | 0.8134 | -0.6774 | 1.0000 | | |
| $Y_{14}$ | -0.0095 | -0.2040 | 0.3746 | -0.2149 | 0.1748 | 0.2587 | 0.2797 | 0.2192 | -0.1559 | 0.1149 | 1.0000 | |
| $Y_{15}$ | 0.1320 | 0.0194 | 0.4355 | -0.4393 | 0.3540 | 0.3906 | 0.5542 | 0.6319 | -0.5433 | 0.7236 | -0.1965 | 1.0000 |

1976. The variables most often included in 1974 to 1975 and 1975 to 1976 were snow hardness and snow density. Snow parameters accounted for 15 of 23 significant variables in 1974 to 1975 and 18 of 33 significant variables in 1975 to 1976 (Table 11).

There appeared to be a good relationship between snowcover density and hardness in 1974 to 1975 (r=.72), but this decreased in 1975 to 1976 (r=.27, Table 12). The variability of mean snowcover thickness measured in 1974 to 1975 was less variable than, and included in the range of the 1975 to 1976 measurements (Table 13). The alder tamarack bog and aspen upland had the thickest snowcover in both winters. Snowcover thickness while being the first significant variable chosen is greatly influenced by changes in barometric pressure and ambient temperature (Table 10B). The effects of these were closely correlated to hardness and density (Table 10) and possibly masked the snow station factors. Also the snowcover measurements were closely associated with time (Table 9 and 10).

These could be indicative of the overall effect of weather on snowcover development. In the analysis of the snow station parameters, F values sufficiently large to be analyzed were obtained in four of six cases in both 1974 to 1975 and 1975 to 1976. Their predictive values were similar to those found for the overall grouping probably because they were often included in the first three significant variables.

TABLE 11

Frequency of occurrence of variables as 3 significant variables in step-wise discriminant analysis of 6 study plots in winters 1974-75 and 1975-76

| Year and variable | No. of times included in first 3 significant variables (excluding $Y_5$) |
|---|---|
| 1974-75: $Y_2$ | 1 |
| $Y_3$ | 2 |
| $Y_7$ | 3 |
| $Y_8$ | 0 |
| $Y_9$ | 1 |
| $Y_{10}$ | 5 |
| $Y_{11}$ | 2 |
| $Y_{12}$ | 4 |
| $Y_{13}$ | 3 |
| $Y_{14}$ | 1 |
| $Y_{15}$ | 1 |
| Total | 23 |
| 1975-76: $Y_2$ | 2 |
| $Y_3$ | 4 |
| $Y_4$ | 3 |
| $Y_7$ | 4 |
| $Y_8$ | 1 |
| $Y_9$ | 2 |
| $Y_{10}$ | 4 |
| $Y_{11}$ | 6 |
| $Y_{12}$ | 2 |
| $Y_{13}$ | 2 |
| $Y_{14}$ | 2 |
| $Y_{15}$ | 1 |
| Total | 33 |

TABLE 12

Mean, standard deviation and correlation coefficient of snow hardness ($g/cm^2$) and snow density $g/cm^3$) in both winters

| | Number of readings | $\bar{X}$ | SD | Correlation coefficient (r) |
|---|---|---|---|---|
| 1974-75 | | | | |
| Hardness | 269 | 226.7700 | 373.9700 | 0.7218 |
| Density | 267 | 237.8800 | 51.1800 | |
| 1975-76 | | | | |
| Hardness | 265 | 265.3018 | 671.0449 | 0.2728 |
| Density | 265 | 192.7207 | 41.1680 | |

TABLE 13

Snowcover thickness (cm) with standard error and range in each habitat for 1974-75 and 1975-76

| | Number of readings | Missing readings | $\bar{X}$ | SE |
|---|---|---|---|---|
| 1974-75 | | | | |
| Alder tamarack bog | 99 | 36 | 35.5 | 1.9 |
| Alder ridge ecotone | 98 | 37 | 28.7 | 1.5 |
| Aspen upland | 94 | 41 | 35.4 | 1.7 |
| Black spruce bog | 51 | 24 | 32.4 | 2.1 |
| Jackpine ridge | 51 | 24 | 28.6 | 1.9 |
| Jackpine sandplain | 22 | 8 | 31.3 | 3.5 |
| 1975-76 | | | | |
| Alder tamarack bog | 100 | 10 | 38.5 | 0.9 |
| Alder ridge ecotone | 104 | 6 | 31.0 | 1.1 |
| Aspen upland | 102 | 8 | 36.6 | 1.0 |
| Black spruce bog | 55 | 0 | 29.5 | 1.0 |
| Jackpine ridge | 53 | 2 | 22.9 | 1.7 |
| Jackpine sandplain | 22 | 0 | 28.5 | 1.7 |

Three of the factors thought to have the greatest influence on $CO_2$ accumulation: subnivean temperature, snowcover thickness and ice layers in the snow profile; were tested against the $CO_2$ groups in each of the six plots in both years (Table 7 and 8). In only one case, the black spruce bog, did the predictive value increase markedly (55 to 78%) but in the alder tamarack bog there was a marked decrease (69 to 18%) in predictive value. Therefore the combination of these three factors was not effective in predicting $CO_2$ concentrations. In only one case was subnivean temperature found to have significant effect on the percentage of "groups" correctly classified. Subnivean temperature was not as significant a contributor to a predictive value as the snow characteristics especially snowcover thickness.

The mean subnivean temperatures for both winters were very similar, but the correlation coefficients showing the relationship between it and $CO_2$ concentrations were quite different for the two winters (Table 14). So some other environmental factor must have influenced the correlation. The winter of 1974 to 1975 had colder mean temperatures than 1975 to 1976 in all habitats except the alder ridge ecotone where it was $0.3^{o}$C. warmer (Table 15). This is within the region of error of the thermometer. The aspen upland had the highest mean subnivean temperatures in both winters. The black spruce bog and jackpine ridge had the lowest subnivean temperatures in 1974 to 1975 and 1975 to 1976.

TABLE 14

Mean, standard deviation and Pearson correlation coefficient of $CO_2$ (%/volume) and subnivean temperature (°C.) in the winters of 1974 to 1975 and 1975 to 1976 using SPSS

| | Number of Measurements | $\bar{X}$ | SD | Correlation coefficient |
|---|---|---|---|---|
| 1974-75 | | | | |
| $CO_2$ (%/volume) | 550 | .0259 | .0132 | 0.1990 |
| Subnivean temperature (°C) | 250 | -4.88 | 2.10 | |
| 1975-76 | | | | |
| $CO_2$ (%/volume) | 434 | .0263 | .0116 | 0.5415 |
| Subnivean temperature (°C) | 436 | -4.20 | 3.21 | |

TABLE 15

Subnivean mean temperatures ($^{o}C.$) with standard error and range in each habitat for 1974-75 and 1975-76

| | No. of readings. | Missing readings | $\bar{X}$ | SE |
|---|---|---|---|---|
| 1974-75 | | | | |
| Alder tamarack bog | 75 | 60 | -5.21 | 0.24 |
| Alder ridge ecotone | 76 | 59 | -4.53 | 0.23 |
| Aspen upland | 44 | 91 | -3.20 | 0.22 |
| Black spruce bog | 24 | 51 | -6.65 | 0.38 |
| Jackpine ridge | 14 | 61 | -5.89 | 0.44 |
| Jackpine sandplain | 17 | 13 | -5.94 | 0.30 |
| 1975-76 | | | | |
| Alder tamarack bog | 110 | 0 | -4.32 | 0.27 |
| Alder ridge ecotone | 106 | 4 | -4.83 | 0.34 |
| Aspen upland | 108 | 2 | -2.98 | 0.25 |
| Black spruce bog | 50 | 5 | -4.46 | 0.49 |
| Jackpine ridge | 42 | 13 | -5.13 | 0.59 |
| Jackpine sandplain | 20 | 2 | -4.28 | 0.69 |

The site-dependent factors (change in microtopography, thickness of soil and percentage of green ground cover) did not influence the predictive value consistently between plots or years when tested alone or with other environmental parameters, although they should have been what determined $CO_2$ production. This suggests that the most important site-dependent parameters were not measured. Site-independent factors contributed to the predictive values to the greatest degree. The formation of the snow layer was important in contributing to the predictive value. Snow density, hardness and thickness were especially important in association with $CO_2$ accumulation.

SECTION 3.

## EFFECT OF $CO_2$ ON SMALL MAMMAL DISTRIBUTION

### SMALL MAMMAL NUMBERS

The total numbers of small mammals of the eight species caught during this study are shown in Table 16. *Microsorex hoyi* is not listed because it was not possible to differentiate between it and *Sorex cinereus* in the field. All individuals of these two species were labelled *Sorex cinereus*. The most frequently captured species was *Clethrionomys gapperi*; its numbers were greater than all the other species combined. *Microtus pennsylvanicus* was the second most common species in 1975 to 1976. For the other trapping periods

TABLE 16

Number of small mammals live-trapped in the summers of 1974, 1975 and 1976 and throughout the study.

| SPECIES | JUNE-SEPT. 73 | MAY-SEPT. 74 | MAY-SEPT. 74 & DEC. 74-Apr. 75 | MAY-SEPT. 75 | MAY-SEPT. 75 and OCT. 75 - APR.76 |
|---|---|---|---|---|---|
| *Clethrionomys gapperi* | 44 | 109 | 109 | 198 | 239 |
| *Microtus pennsylvanicus* | 1 | 2 | 2 | 3 | 36 |
| *Peromyscus maniculatus* | 6 | 11 | 11 | 11 | 11 |
| *Zapus hudsonius* | 0 | 1 | 1 | 2 | 2 |
| *Sorex cinereus* | 2 | 17 | 17 | 2 | 6 |
| *S. arcticus* | 0 | 0 | 0 | 0 | 1 |
| *Blarina brevicauda* | 10 | 20 | 20 | 3 | 3 |
| *Synaptomys borealis* | 0 | 0 | 0 | 2 | 2 |
| number live-trapped | 63 | 160 | 160 | 221 | 300 |
| number trap nights | 4000 | 5400 | 7100 | 8700 | 10,960 |

(summer 1973 and 1974 to 1975) *Peromyscus maniculatus*, *S. cinereus* and *Blarina brevicauda* were the next most common species and had greater numbers captured than *Microtus*.

The total number of individuals captured in 1975 to 1976 was greater than in either of the other two years. *Clethrionomys* and *Microtus* increased markedly in number from 1973 to 1976. *Synaptomys borealis* and *Sorex arcticus* were captured for the first time in 1975 to 1976. *Peromyscus* numbers were similar in 1975 to 1976 to the other years. *Zapus hudsonius* was rarely captured. *Sorex cinereus* and *Blarina* captures dropped markedly from their greatest numbers in 1974 to 1975. The decreases and stationary numbers are even more significant because there was an increase in trap nights (Table 17; $p < 0.005$) No new animals were added to the total during the winter of 1974 to 1975, in contrast to the winter of 1975 to 1976 when there was a marked increase in new individuals trapped, particularly *Clethrionomys* and *Microtus* (Table 16).

The numbers of small mammals captured per 100 trap nights in each month in each habitat can be seen in Table 18. *C. gapperi* and *P. maniculatus* were captured in all plots. *M. pennsylvanicus* was captured in the alder tamarack bog, alder ridge ecotone and aspen upland. *S. cinereus* and *B. brevicauda* were captured in all habitats except the jackpine sandplain. *S. arcticus* was captured once in the alder tamarack bog. *Synaptomys borealis* was captured rarely in the alder tamarack bog and alder ridge ecotone. *Z. hudsonius* was

TABLE 17

Significance of difference of number of captures of small mammals in 1973-76

| | Trap nights | Observed captures | Expected captures | $\chi^2$ |
|---|---|---|---|---|
| 1973 | 4,000 | 63 | 63.00 | 0 (p = 0, df = 2) |
| 1974-75 | 7,100 | 160 | 111.80 | 20.780 (p<0.005, df = 2) |
| 1975-76 | 10,960 | 300 | 172.62 | 93.996 (p<0.005, df = 2) |

TABLE 18

Total number of live-trapped captures/100 trap nights on six study plots throughout the study

| | *Clethrionomys gapperi* | *Microtus pennsylvanicus* | *Peromyscus maniculatus* | *Sorex cinereus* | *S. arcticus* | *Synaptomys borealis* | *Blarina brevicauda* | *Zapus hudsonius* |
|---|---|---|---|---|---|---|---|---|
| Jackpine sandplain | | | | | | | | |
| September 1974 | 1.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| May 1975 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| June 1975 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1975 | 0.0 | 0.0 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1975 | 0.0 | 0.0 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| September 1975 | 0.0 | 0.0 | 6.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Jackpine ridge | | | | | | | | |
| August 1973 | 4.3 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 |
| June 1974 | 6.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1974 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1974 | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| September 1974 | 10.0 | 0.0 | 1.0 | 1.7 | 0.0 | 0.0 | 0.7 | 0.0 |
| May 1975 | 4.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| June 1975 | 3.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1975 | 8.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1975 | 3.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| September 1975 | 6.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Black spruce bog | | | | | | | | |
| August 1973 | 3.3 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 1.0 | 0.0 |
| June 1974 | 0.7 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1974 | 6.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1974 | 5.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 |
| December 1974 | 6.7 | 0.0 | 0.0 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| February 1975 | 4.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| March 1975 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1975 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1975 | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| September 1975 | 4.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| November 1975 | 25.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| January 1976 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| February 1976 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| April 1976 | 3.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Alder tamarack bog | | | | | | | | |
| September 1973 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.4 | 0.0 |
| May 1974 | 7.0 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 |
| June 1974 | 4.3 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1974 | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1974 | 9.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.7 | 0.0 |
| September 1974 | 9.0 | 0.0 | 0.0 | 1.7 | 0.0 | 0.0 | 3.3 | 0.0 |
| December 1974 | 17.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| January 1975 | 2.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| February 1975 | 2.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| March 1975 | 4.0 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| April 1975 | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| May 1975 | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 |
| June 1975 | 7.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1975 | 19.0 | 0.3 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1975 | 7.7 | 0.7 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| September 1975 | 12.7 | 2.0 | 0.0 | 0.7 | 0.0 | 0.7 | 0.0 | 0.0 |
| November 1975 | 9.3 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 |
| December 1975 | 3.7 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| January 1976 | 1.7 | 2.7 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 |
| February 1976 | 1.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| March 1976 | 3.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| April 1976 | 1.7 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

. . . continued

TABLE 18 (CONTINUED)

| | *Clethrionomys gapperi* | *Microtus pennsylvanicus* | *Peromyscus maniculatus* | *Sorex cinereus* | *S. arcticus* | *Synaptomys borealis* | *Blarina brevicauda* | *Zapus hudsonius* |
|---|---|---|---|---|---|---|---|---|
| Alder ridge ecotone | | | | | | | | |
| September 1974 | 5.3 | 0.3 | 1.3 | 0.3 | 0.0 | 0.0 | 1.3 | 0.0 |
| December 1974 | 6.7 | 0.0 | 0.0 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| February 1975 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| April 1975 | 2.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| May 1975 | 4.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| June 1975 | 11.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1975 | 8.3 | 1.3 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.3 |
| August 1975 | 12.0 | 3.3 | 0.7 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| September 1975 | 6.3 | 0.7 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| October 1975 | 25.3 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 |
| November 1975 | 13.3 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| December 1975 | 5.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| January 1976 | 0.0 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| February 1976 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| April 1976 | 5.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Aspen upland | | | | | | | | |
| July 1973 | 2.1 | 0.1 | 2.7 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 |
| July 1974 | 3.7 | 0.0 | 2.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1974 | 3.3 | 0.0 | 1.7 | 0.0 | 0.0 | 0.0 | 1.7 | 0.0 |
| September 1974 | 1.7 | 0.0 | 1.7 | 0.3 | 0.0 | 0.0 | 2.0 | 0.0 |
| December 1974 | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| January 1975 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| May 1975 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| June 1975 | 0.0 | 0.0 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| July 1975 | 4.7 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| August 1975 | 7.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| October 1975 | 20.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| November 1975 | 16.1 | 2.8 | 0.0 | 1.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| December 1975 | 11.4 | 2.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| January 1976 | 3.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| February 1976 | 5.6 | 2.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| March 1976 | 5.6 | 7.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| April | 2.8 | 3.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

captured rarely in the alder ridge ecotone and black spruce bog.

There is a significant decrease ($p<0.05$) in the numbers of captures after the fall critical period (onset of the hiemal threshold) in some plots both years and in only one winter in others (Table 19). The aspen upland and black spruce bog showed no significant change in the number of captures in 1974 to 1975, there being few captures during this period in these two plots. The alder tamarack bog and alder ridge ecotone showed a significant decrease ($p<0.01$) in numbers of captures before and after the hiemal threshold. In the winter of 1975 to 1976 all plots, except the aspen upland ($p<0.05$), showed a significant decrease ($p<0.01$) in numbers of captures during the fall critical period.

## MOVEMENT OF SMALL MAMMALS IN RELATION TO $CO_2$ ACCUMULATION

Figures 8 to 10 show the distribution of small mammal captures in the aspen upland, alder ridge ecotone and the alder tamarack bog. The microtopography of the aspen upland is varied with areas of rock, thick soil ($>25$ cm) and shallow soil ($<25$ cm). The thick soils, particularily from A5-A8 to D5-D8, were associated with the greatest $CO_2$ accumulation. Before the $CO_2$ concentrations started to increase in January there was a significant number of captures in that area whereas after accumulation there were no captures and those on the rock, shallow and remainder of the deep soil (zones of lesser $CO_2$) were relatively increased. Once the snow melted and subnivean air mixed with environmental air, a marked animal that had frequented that area, before increased $CO_2$ concentrations, was recaptured there.

TABLE 19

Significance of change in number of small mammals' trap captures and trap failures before (included captures in the months before in which the hiemal threshold was broken) and after hiemal threshold (included all months when the hiemal threshold was established)

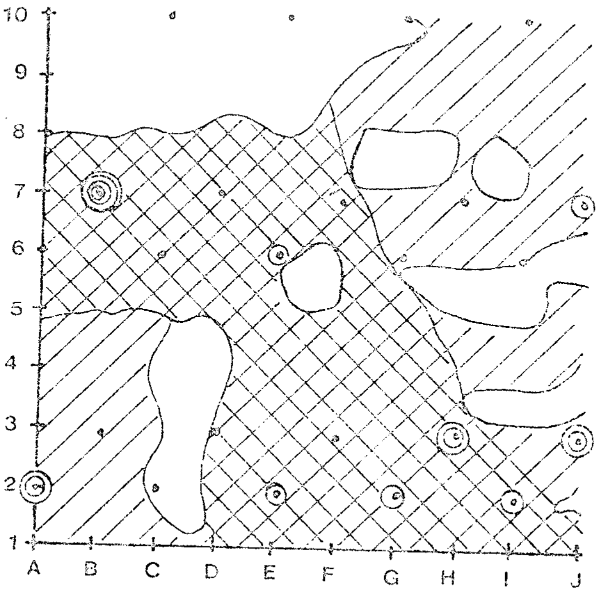
| habitat and period | No. captures | No. failures | No. captures | No. failures | Significance | $x^2$ | df |
|---|---|---|---|---|---|---|---|
| | Before hiemal threshold | | After hiemal threshold | | | | |
| Aspen upland | | | | | | | |
| 1974-75 | 4 | 146 | 1 | 224 | $p=0$ | 3.4 | 1 |
| 1975-76 | 57 | 333 | 27 | 288 | $p<0.05$ (almost $p<0.01$) | 6.0 | 1 |
| Alder tamarack bog | | | | | | | |
| 1974-75 | 17 | 133 | 8 | 217 | $p<0.01$ | 8.7 | 1 |
| 1975-76 | 54 | 171 | 31 | 194 | $p<0.01$ | 7.7 | 1 |
| Alder ridge ecotone | | | | | | | |
| 1974-75 | 7 | 143 | 1 | 224 | $p<0.01$ | 7.7 | 1 |
| 1975-76 | 44 | 301 | 4 | 266 | $p<0.01$ | 32.1 | 1 |
| Black spruce bog | | | | | | | |
| 1974-75 | 6 | 144 | 4 | 221 | $p=0$ | 1.7 | 1 |
| 1975-76 | 26 | 244 | 4 | 266 | $p<0.01$ | 17.1 | 1 |

FIGURE 8

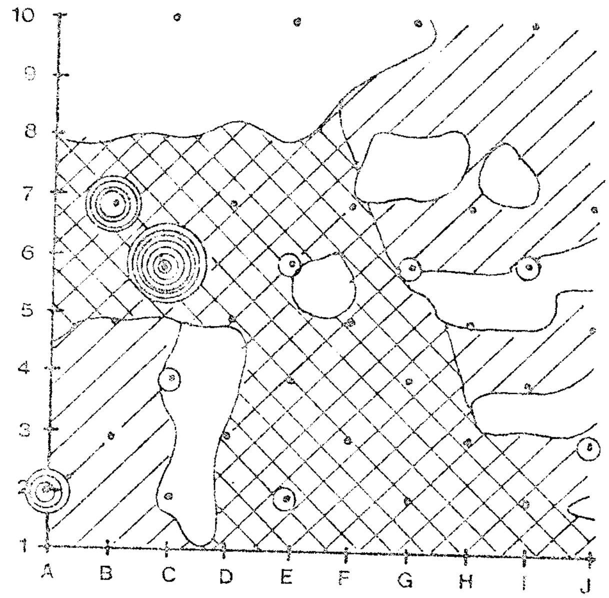
DISTRIBUTION OF SMALL MAMMAL CAPTURES IN THE ASPEN UPLAND FROM OCTOBER 1975 TO APRIL 1976.

- rock
- shallow soil ( 25 cm)
- deep soil ( 25 cm)
- capture
- trap site

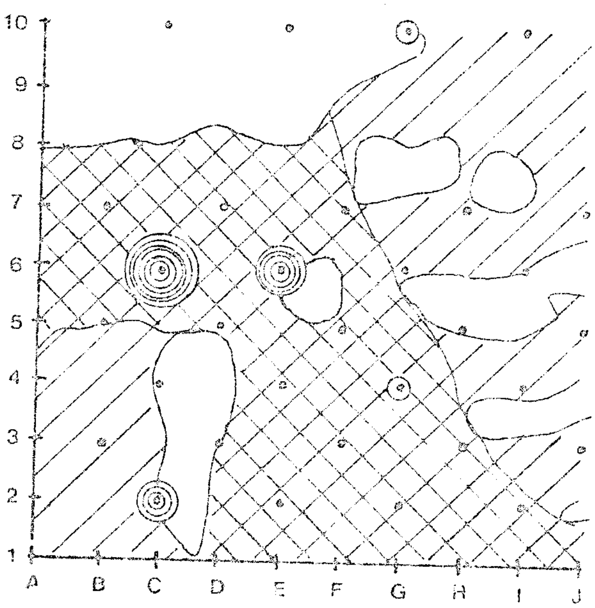
Concentric circles = number of captures per site



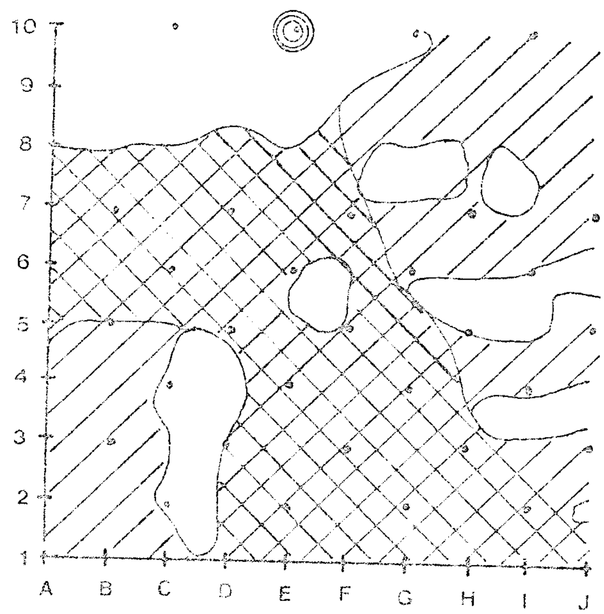

OCTOBER




NOVEMBER

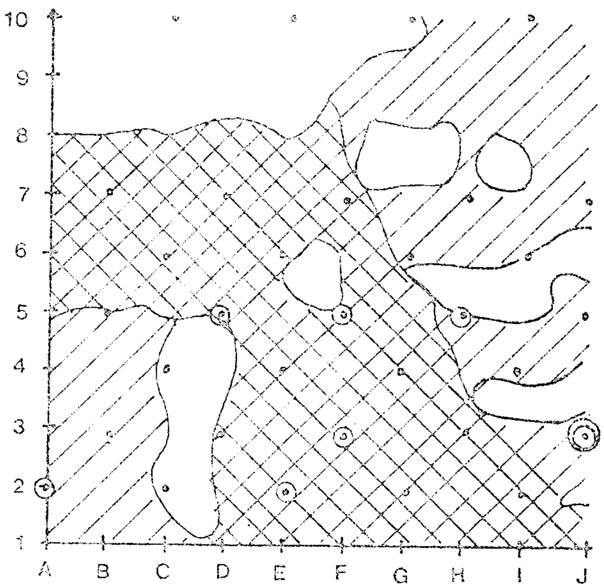



DECEMBER

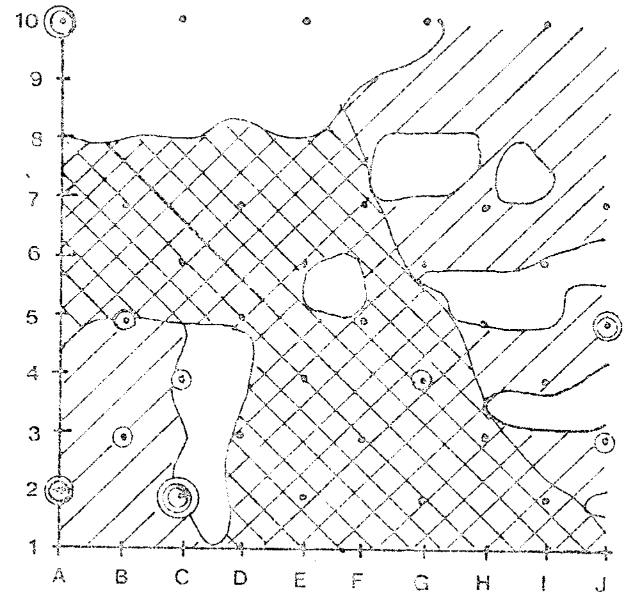



JANUARY

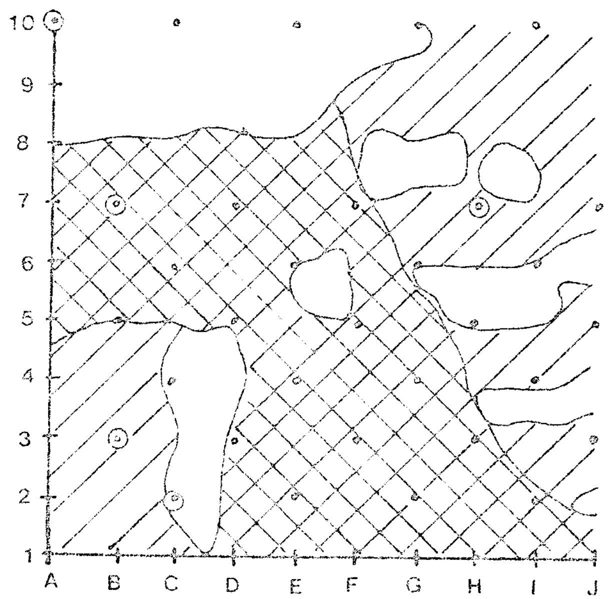
HIEMAL THRESHOLD ESTABLISHED




FEB.




MARCH




APRIL

HIEMAL THRESHOLD BROKEN

FIGURE 9.

DISTRIBUTION OF SMALL MAMMAL CAPTURES IN THE ALDER RIDGE ECOTONE FROM OCTOBER 1975 TO MAY 1976. (THE MONTH OF MARCH 1976 WAS OMITTED FROM THE FIGURE BECAUSE NO CAPTURES WERE MADE IN THAT MONTH).

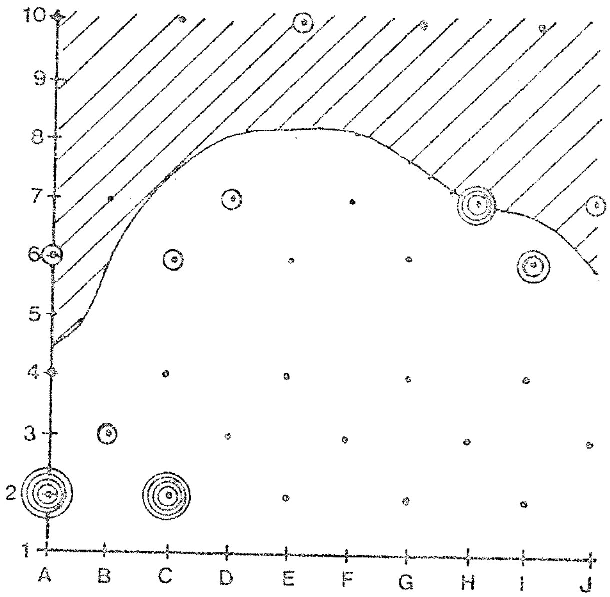
☐ rock ridge

▨ bog

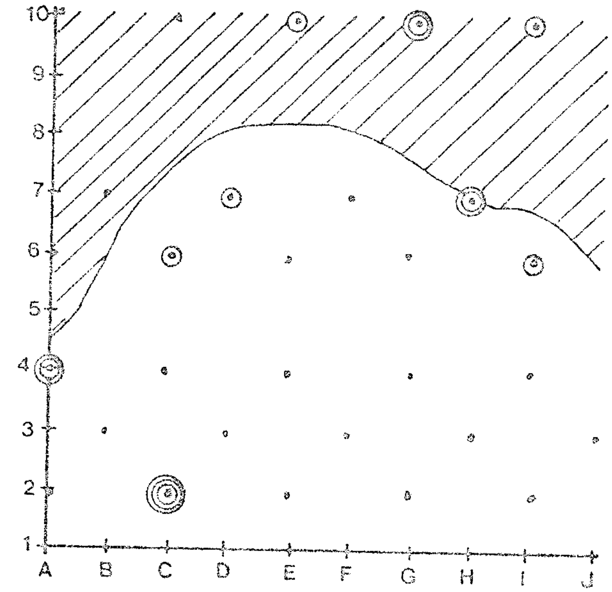
○ small mammal capture

● trap site

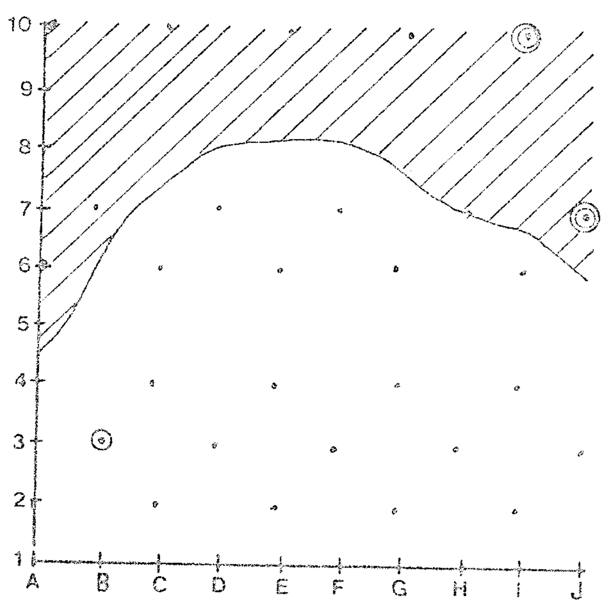
Concentric circles = number of captures per site



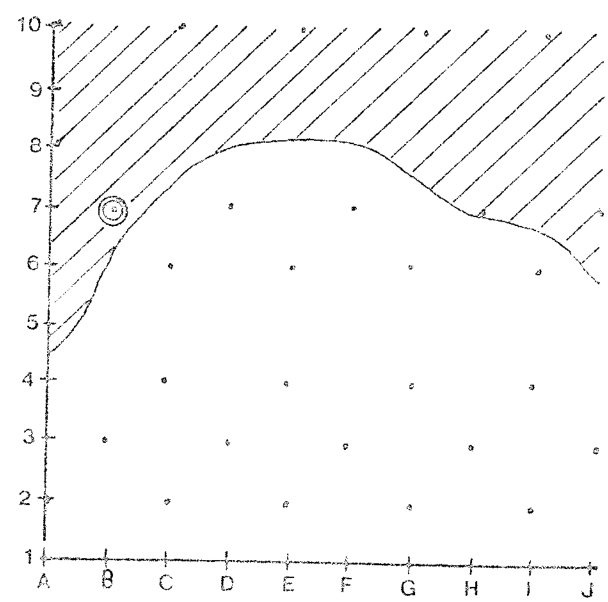

OCTOBER



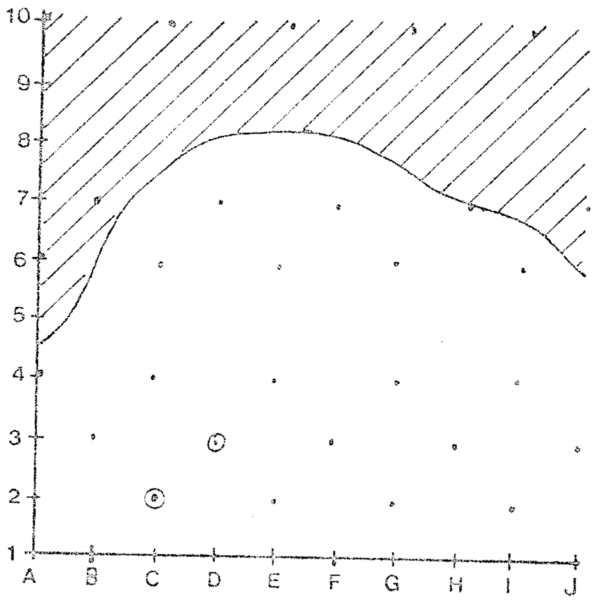

NOVEMBER



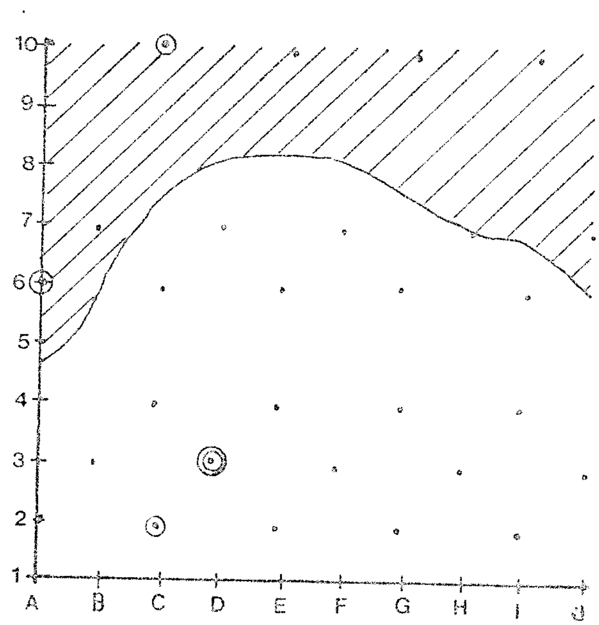

DECEMBER




JANUARY




FEBUARY




APRIL

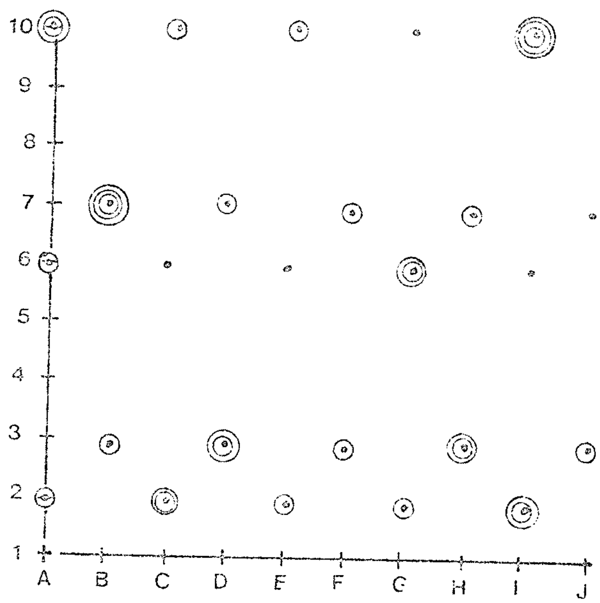
FIGURE 10.

DISTRIBUTION OF SMALL MAMMAL CAPTURES IN THE ALDER TAMARACK BOG FROM NOVEMBER 1975 TO APRIL 1976.

○ small mammal capture

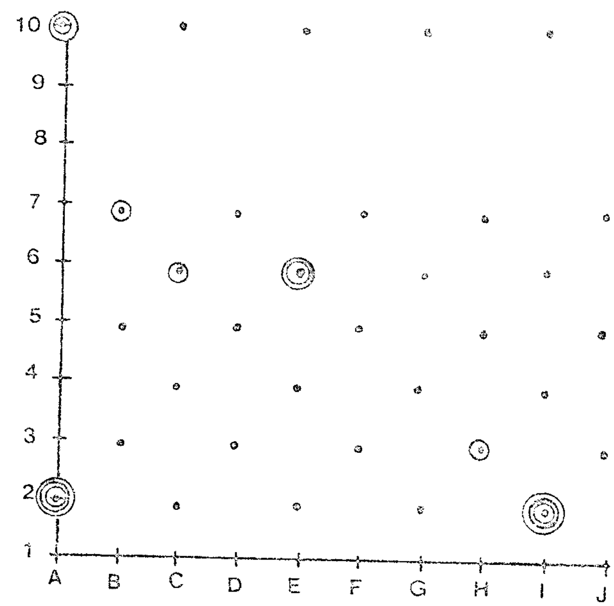
◍ trap site

Concentric circles = number of captures per site



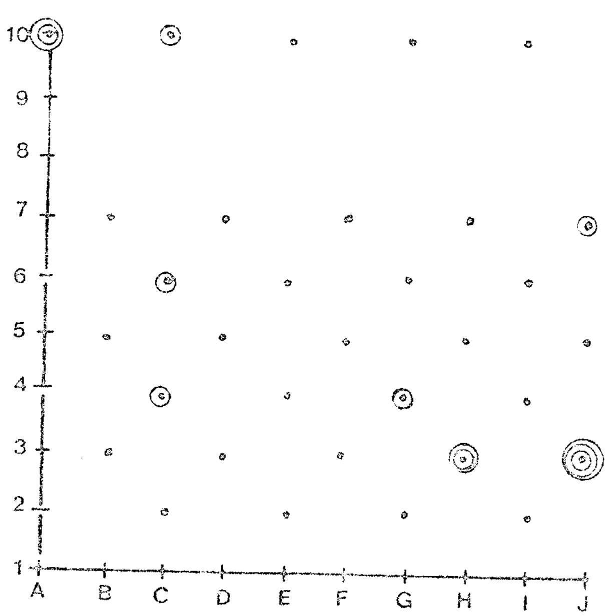

NOVEMBER

FALL CRITICAL PERIOD

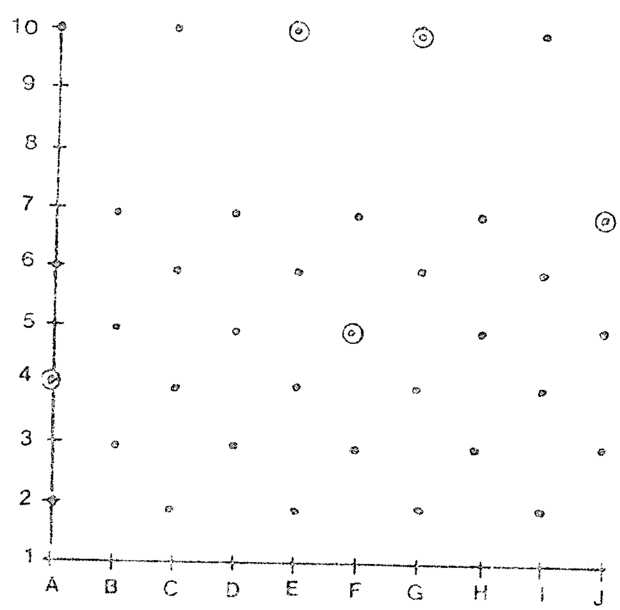



DECEMBER

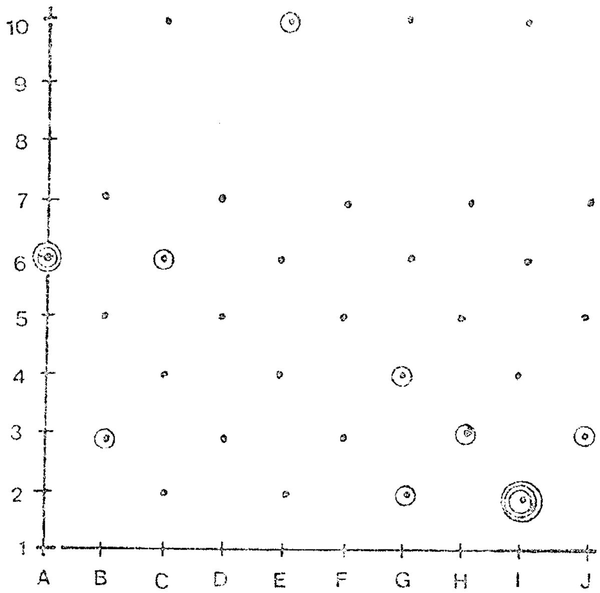
HIEMAL THRESHOLD ESTABLISHED



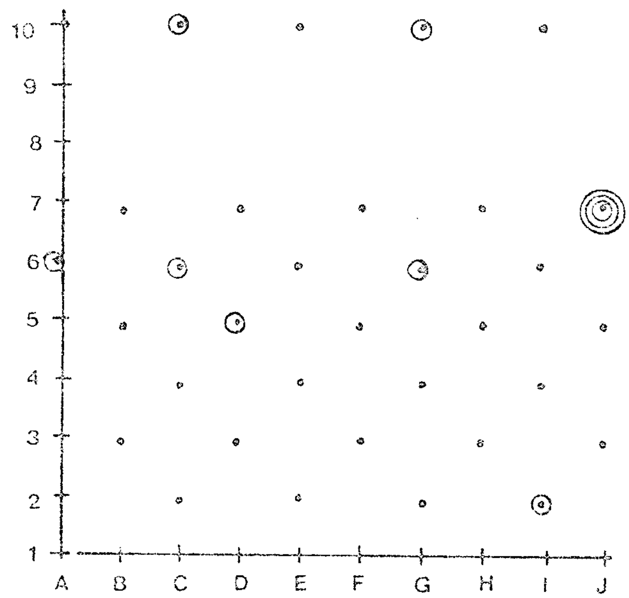

JANUARY




FEBRUARY




MARCH




APRIL

HIEMAL THRESHOLD BROKEN

In the aspen plot four animals were caught quite frequently from October to January or later. Clethrionomys #530 was a young female caught first in August 1975. During August and November this animal was found in the area of the plot which later would have the greatest $CO_2$ concentration. In October it was captured in areas with thin soil. In February and March it was captured only in one area with thin soil at the edge of a bare rock. The area with thick soil and greater $CO_2$ concentrations was part of its home range in the late autumn prior to the fall critical period but not once $CO_2$ had started to accumulate.

Clethrionomys #9 was a young female first captured in October 1975. She was eventually captured 12 times from October to December in the area where an unusually great $CO_2$ concentration would eventually be measured. In January when $CO_2$ started to accumulate in the areas of thick soil this vole was captured on the rock ridge where no $CO_2$ accumulation occured. Unfortunately she died in the trap.

Clethrionomys #41 was a female captured first in November. She was caught nine times in November and December in the area which later showed the greatest $CO_2$ accumulation but in January and March she was captured a total of three times only on rock ridges. In April she was captured once on a ridge and once back in the area where she had been captured originally nine times before $CO_2$ had started to accumulate.

*Clethrionomys* #1 was a female first captured in October 1975. In October and November she was captured four times in the area where $CO_2$ would accumulate to the greatest extent. In December she was captured once in the area with thin soil and in January on a rock ridge.

These four voles avoided the area where $CO_2$ was to accumulate to its maximum extent as soon as it started to do so. One vole was found dead, two others disappeared entirely from the plot and the one that survived through the spring critical period returned to the area that had once held the greatest amount of $CO_2$. The area of greatest $CO_2$ concentration was part of their home range but was utilized only when $CO_2$ was low.

The alder ridge ecotone was generally divided into two areas, ridge and bog (Figure 9). $CO_2$ did accumulate to some extent in 1975 to 1976. The number of small mammals captured after the fall critical period markedly decreased (November: 7 animals, December: 5 animals; critical period; January and February: 1 animal each; March: 0). In April the number of voles captured increased to four, one of which, *Clethrionomys* #508, a juvenile male who was first captured in October, was recaptured in the same area it had vacated after the November trapping period. It is concluded that the alder ridge was not a good overwintering habitat because only one of the animals regularly captured was there during the winter. *Clethrionomys* #0 was a young female who appeared in February after not being captured since October. The other vole was captured only in January (*Microtus* #40-0 juvenile male). Two of the *Clethrionomys* that left the ridge in November or December had been captured in the bog as well and after the critical period were captured only there. The other voles may have moved into a different part of the adjacent bog that was not part of the study area.

The effects of $CO_2$, habitat and the hiemal threshold were significant ($p < 0.01$) in relation to small mammal captures in the alder ecotone plot (Figure 9). Prior to the hiemal threshold (during the fall critical period) small mammal captures were high in this area. The adjacent bog plot reached the hiemal threshold before the ridge and small mammals were captured there more often than in the ecotone. In January there were two captures in the ecotone area that later had more $CO_2$ but these captures occurred prior to the increased $CO_2$ measurements. In February the same area still had high concentrations of $CO_2$ which small mammals avoided. The two captures recorded were on the ridge areas with reduced amounts of $CO_2$. Most of the greater concentrations of $CO_2$ occurred in March and no small mammals were captured then. The small mammals may have moved into the adjacent bog area with relatively lower $CO_2$. There was a corresponding increase in numbers from February to March in the alder tamarack bog (5 to 12 captures). In April the snowcover disappeared and small mammals were captured again in the alder ecotone plot.

The alder tamarack bog never showed a significant $CO_2$

accumulation, nor marked microtopographical variation, and small mammals exhibited no distinct change of areas occupied in the habitat. (Table 3, 20 and 21, Figure 10). Prior to the onset of the hiemal threshold (November to December) there was a decrease in numbers of captures probably due to the large temperature fluctuations of the fall critical period (Pruitt 1957 ;Fuller et al. 1969).

The black spruce bog has no distinct microtopographic differences but in 1975 to 1976 there were sufficient captures to show a significant effect ($p \leqslant 0.01$) of the fall critical period. Unfortunately there were insufficient small mammal captures after the hiemal threshold was reached to show the exact effect of $CO_2$. Once the hiemal threshold was reached small mammal captures were very low (0 to 2.2 captures/100 trap nights). In March, during the period of greatest $CO_2$ accumulation, there were no captures of small mammals in this area. When the snowcover melted in April captures increased to higher numbers (3.3 captures/100 trap night) than those seen after the hiemal threshold was reached (2.2 captures/ 100 trap nights).

STATISTICAL ANALYSIS OF CHANGES IN SMALL MAMMAL DISTRIBUTION

In the alder tamarack bog a significant decrease ($p \leqslant 0.01$) was seen in the total numbers of small mammals captured before and after the hiemal threshold was established in both 1974 to 1975 and 1975 to

TABLE 20

Significance of number of captures in 3 small mammal trapping lines in alder tamarack bog before and after hiemal threshold

| Date | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | o* | e* | $x^2$ | o* | e* | $x^2$ | o* | e* | $x^2$ |
| December 1974 | 1 | 4.8 | 3.0083 | 7 | 4.8 | 0.300 | 5 | 2.4 | 2.8167 |
| January 1975 | 0 | 0.8 | 0.8000 | 2 | 0.8 | 1.800 | 0 | 0.4 | 0.4000 |
| February 1975 | 1 | 0.8 | 0.0500 | 1 | 0.8 | 0.050 | 0 | 0.4 | 0.4000 |
| March 1975 | 2 | 1.6 | 0.1000 | 1 | 1.6 | 0.225 | 1 | 0.8 | 0.0500 |
| April 1975 | 0 | 1.6 | 1.6000 | 2 | 1.6 | 0.100 | 2 | 0.8 | 1.8000 |
| Totals | | | 5.5583 | | | 2.475 | | | 5.4667 |

df = 8 (non-significant)
1 = lines A - J #2-3, 2 = lines A - J #6-7, 3 = line A - J #10
o* = observed captures
e* = expected captures

TABLE 21

Significance of number of captures in 4 lines of small mammal traps in alder tamarack bog before and after hiemal threshold

| Date | 1 | | | 2 | | | 3 | | | 4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | o | e | $x^2$ | o | e | $x^2$ | o | e | $x^2$ | o | e | $x^2$ |
| November 1975 | 14 | 12.0 | 0.3333 | 9 | 12.0 | 0.7500 | 7 | 6.0 | 0.1667 | | | |
| December 1975 | 8 | 4.3 | 3.1837 | 4 | 4.3 | 0.0209 | 2 | 2.1 | 0.0048 | 1 | 4.3 | 2.5325 |
| January 1976 | 6 | 3.7 | 1.4297 | 2 | 3.7 | 0.7811 | 3 | 1.9 | 0.6368 | 2 | 3.7 | 0.7811 |
| February 1976 | 0 | 1.4 | 1.4000 | 1 | 1.4 | 0.1143 | 2 | 0.7 | 2.4142 | 2 | 1.4 | 0.2571 |
| March 1976 | 8 | 3.7 | 4.9973 | 3 | 3.7 | 0.1324 | 1 | 1.9 | 0.4263 | 1 | 3.7 | 1.9703 |
| April 1976 | 1 | 2.9 | 1.2448 | 6 | 2.9 | 3.3138 | 2 | 1.4 | 0.2571 | 1 | 2.9 | 1.2448 |
| Totals | | | 12.5888 | | | 5.1125 | | | 3.9059 | | | 6.7858 |

df = 12 (p = 0), 1 = lines A - J #2-3, 2 = lines A - J #6-7, 3 = line A - J #10, 4 = lines A - J #4-5

1976 (Table 19). There was no marked microtopographical or vegetation zones in this plot so to test for change in distribution of small mammals each trapping line (A - J) was designated as a different area.

No significant change was observed in small mammal distribution either from December 1974 to April 1975 or November 1975 to April 1976 (Tables 20 and 21).

The black spruce bog exhibited a $CO_2$ accumulation at all five sampling stations as well as a significant decrease ($p < 0.01$) in the numbers of small mammals captured after the hiemal threshold in 1975 to 1976 (Tables 22 and 23). There were insufficient captures in 1974 to 1975 to allow statistical testing (no zeros can occur in marginal cells) and specific areas of $CO_2$ accumulation or lack of it could not be defined due to the homogeneity of the habitat.

Table 22 shows the setup of the test with the observed values and totals for 1975 to 1976. Table 23 shows the test itself using $x^2$. To get the expected values in this case:

$$e_{\text{cell } 111} = \frac{A_1 \cdot B_1 \cdot C_1}{h^2} = \frac{30.540.80}{(1,620)^2} = 5$$

This can be calculated for any number of models that are constructed. Model 1 (1 + A + B + C) of total independence for the black spruce bog was disproved. Model 2 (1 + A + B + C + AB) explaining the distribution due to the effect of the lines accounted for an insignificant amount

TABLE 22

Fienberg's contingency table test for black spruce bog 1975-76: observed values with $A_1$ capture of $A_2$ failure, B = number of the line (i.e., $B_1$ = line I, $B_2$ = line 2, etc.) and $C_1$ = before and $C_2$ = after the hiemal threshold. $A^+$, $B^+$ or $C^+$ = combined values of A &/or B &/or C

| | $C_1$ | | $C_2$ | $C^+$ |
|---|---|---|---|---|
| $A_1B_1$ | 11<br>111 | observed value<br>cell number | 1<br>112 | 12 |
| $A_1B_2$ | 8<br>121 | | 2<br>122 | 10 |
| $A_1B_3$ | 7<br>131 | | 1<br>132 | 8 |
| $A_2B_1$ | 259<br>211 | | 269<br>212 | 528 |
| $A_2B_2$ | 262<br>221 | | 268<br>222 | 530 |
| $A_2B_3$ | 263<br>231 | | 269<br>232 | 532 |
| $A_1B^+$ | 26 | | 4 | 30 |
| $A_2B^+$ | 784 | | 806 | 1,590 |
| $A^+B_1$ | 270 | | 270 | 540 |
| $A^+B_2$ | 270 | | 270 | 540 |
| $A^+B_3$ | 270 | | 270 | 540 |
| $A^+B^+$ | 810 | | 810 | 1,620 |

TABLE 23

Fienberg's contingency table test for black spruce bog 1975-76: $\chi^2$ values

| Cell | Observed no. captures | Expected no. of captures | $\chi^2$ | Expected no. of captures | $\chi^2$ | Expected no. of captures | $\chi^2$ |
|---|---|---|---|---|---|---|---|
| | | . . Model 1* . . | | . . Model 2** . . . | | . . Model 3*** . . | |
| 111 | 11 | 5 | 7.2000 | 6 | 4.1667 | 10.4 | 0.0346 |
| 112 | 1 | 5 | 3.2000 | 6 | 4.1667 | 1.6 | 0.2250 |
| 121 | 8 | 5 | 1.8000 | 5 | 1.8000 | 8.7 | 0.0563 |
| 122 | 2 | 5 | 1.8000 | 5 | 1.8000 | 1.3 | 0.3769 |
| 131 | 7 | 5 | 0.8000 | 4 | 2.2500 | 6.9 | 0.0014 |
| 132 | 1 | 5 | 3.2000 | 4 | 2.2500 | 1.1 | 0.0091 |
| 211 | 259 | 265 | 0.1358 | 264 | 0.0947 | 260.3 | 0.0065 |
| 212 | 269 | 265 | 0.0604 | 264 | 0.0947 | 267.7 | 0.0063 |
| 221 | 262 | 265 | 0.0340 | 265 | 0.0340 | 261.3 | 0.0019 |
| 222 | 268 | 265 | 0.0340 | 265 | 0.0340 | 268.7 | 0.0018 |
| 231 | 263 | 265 | 0.0151 | 266 | 0.0338 | 262.3 | 0.0003 |
| 232 | 269 | 265 | 0.0604 | 266 | 0.0338 | 269.7 | 0.0018 |
| | | | 18.3397 (df = 7) | | 16.0365 (df = 1) | | 0.7219 (df = 1) |

Model 1 vs. Model 2: $\chi^2 = 1.5813$ (df = 2, p = 0)

Model 2 vs. Model 3: $\chi^2 = 16.0365$ (df = 1, p = 0.01)

*Model 1: 1 + A + B + C
**Model 2: 1 + A + B + C + AB
***Model 3: 1 + A + B + C + AB + AC

of the variation ($x^2$ = 1.5813, df = 2). Model 3 (1 + A + B + C + AB + AC) explaining the variation in distribution due to the onset of the hiemal threshold accounted for a significant portion ($p<0.01$) of the variation ($x^2$ = 16.0364, df = 1) with a non-significant remainder. This showed that the critical period was very significant in determining small mammal distribution. It can be seen from Table 18 that almost all the small mammals disappeared from the plot at that time. Thus the distribution or lack of small mammal captures after the hiemal threshold was established was due to the fall critical period.

If it had been possible to get more accurate and greater numbers of small mammal captures along the lines then a test of the effect of $CO_2$ on small mammals' distribution would have been possible.

The alder ridge ecotone showed a significant effect ($p<0.01$) of the fall critical period on numbers of captures in both 1974 to 1975 and 1975 to 1976. It also had an accumulation of $CO_2$ at certain times (Table 6) and a marked microtopographical division into two areas. Given these factors a test for the effect of $CO_2$ on distributions of small mammals could be set up for 1975 to 1976. There were insufficient captures in 1974 to 1975. Fienberg's (1970) test, as explained for the black spruce bog, was used. Greater $CO_2$ concentrations are defined as readings greater than ambient levels more than 33.3 % of the time in the entire area of the habitat being studied. Table 24 gives the observed values and Table 25 shows the test. Model 2 showing the effect of $CO_2$ on habitat accounted for a

TABLE 24

Fienberg's contingency table test for alder ridge ecotone 1975-76: observed values

| | $C_1$ | | $C_2$ | $C^+$ |
|---|---|---|---|---|
| $A_1B_1$ | 2<br>111 | Number in that cell<br>Cell Number | 0<br>112 | 2 |
| $A_1B_2$ | 6<br>121 | | 6<br>122 | 12 |
| $A_2B_1$ | 70<br>211 | | 66<br>212 | 136 |
| $A_2B_2$ | 42<br>221 | | 192<br>222 | 234 |
| $A_1B^+$ | 8 | | 6 | 14 |
| $A_2B^+$ | 112 | | 258 | 370 |
| $A^+B_1$ | 72 | | 66 | 138 |
| $A^+B_2$ | 48 | | 198 | 246 |
| $A^+B^+$ | 120 | | 264 | 384 |

$A_1$ = trap captures, $A_2$ = Trap failure, $B_1 = CO_2 >$ .02%/volume, $B_2 = CO_2 \leq$ .02%/volume, C = habitats ($C_1$ bog, $C_2$ rock), A+, B+, C+ - combined values of letter involved.

TABLE 25

Fienberg's contingency table test for alder ridge ecotone 1975-76: $\chi^2$ values

| Cell | Observed no. of captures | Model 1* Expected no. of captures | Model 1* $\chi^2$ | Model 2** Expected no. of captures | Model 2** $\chi^2$ | Model 3*** Expected no. of captures | Model 3*** $\chi^2$ | Model 4**** Expected no. of captures | Model 4**** $\chi^2$ |
|---|---|---|---|---|---|---|---|---|---|
| 111 | 2 | 1.6 | 0.1000 | 2.6 | 0.1385 | 4.8 | 1.6333 | 1.6 | 0.1000 |
| 112 | 0 | 3.5 | 3.5000 | 2.4 | 2.4000 | 1.5 | 1.5000 | 0.4 | 0.4000 |
| 121 | 6 | 2.8 | 3.6571 | 1.8 | 9.8000 | 3.2 | 2.4500 | 6.4 | 0.0250 |
| 122 | 6 | 6.2 | 0.0065 | 7.2 | 0.2000 | 4.5 | 0.5000 | 5.6 | 0.0286 |
| 211 | 70 | 41.6 | 19.3885 | 69.4 | 0.0052 | 67.2 | 0.1167 | 70.4 | 0.0023 |
| 212 | 66 | 91.4 | 7.0586 | 63.6 | 0.0906 | 64.5 | 0.0349 | 65.6 | 0.0024 |
| 221 | 42 | 74.1 | 13.9057 | 46.3 | 0.3994 | 44.8 | 0.1750 | 41.6 | 0.0038 |
| 222 | 192 | 163.0 | 5.1595 | 190.8 | 0.0170 | 193.5 | 0.0116 | 192.4 | 0.0008 |
| | | | 52.7759 (df = 4) | | 13.0502 (df = 3) | | 6.4215 (df = 2) | | 0.5629 (df = 1) |

Model 1 vs. Model 2: $\chi^2 = 39.7252$ (df = 1, p = 0.01)

Model 2 vs. Model 3: $\chi^2 = 6.6292$ (df = 1, p = 0.05)

Model 3 vs. Model 4: $\chi^2 = 5.8585$ (df = 1, p = 0.05)

*Model 1: 1 + A + B + C
**Model 2: 1 + A + B + C + BC
***Model 3: 1 + A + B + C + BC + AC
****Model 4: 1 + A + B + C + BC + AC + AB

significant amount ($p<0.01$) of the variation ($x^2 = 39.7$, df = 1). That is, $CO_2$ was closely related to habitat. Model 3 (1 + A + B + C + BC + AC) showing the effect of $CO_2$ on captures again accounted for a significant portion ($p<0.01$) of the variation ($x^2 = 6.6$, df = 1). When the effect of habitat on captures was included (Model 4: 1 + A + B + C + BC + AC + AB) it accounted for a significant part ($p<0.05$) of the variation ($x^2 = 5.9$, df = 1); an insignificant remainder of variation was left. $CO_2$ and habitat were related and both has significant effects ($p<0.01$) on numbers of captures.

In the aspen upland the fall critical period had no significant effect on numbers of captures in 1974 to 1975 but did ($p<0.05$) in 1975 to 1976. $CO_2$ accumulation occurred in both winters (Tables 3 and 4) in this plot and a microtopographical variation was obvious. This variation resulted in three distinct types of areas: rock, shallow soils and deep soils. There were not enough captures in 1974 to 1975 to allow statistical analysis. For the 1975 to 1976 data Fienberg's (1970) test was used (Table 26 and 27). Model 1 (1 + A + B + C) of complete independence was disproved. Model 2 (1 + A + B + C + BC) shows the relationship of $CO_2$ with habitat which accounted for a significant amount of the variation ($x^2 = 10.6$, df = 3). Model 3 (1 + A + B + C + BC + AC) showing the effect of $CO_2$ on captures again accounted for a significant portion of the variation ($x^2 = 7.5$, df = 2). When the effect of habitat on captures was also included (Model 4: 1 + A + B + C + BC + AC + AB) it accounted for a significant part of the variation ($x^2 = 5.8$, df = 1). $CO_2$ levels and habitat was related

TABLE 26

Fienberg's contingency table test for aspen upland 1975-76: observed values

| | $C_1$ | $C_2$ | $C_3$ | $C^+$ |
|---|---|---|---|---|
| $A_1B_1$ | 9<br>111 | 8<br>112 | 6<br>113 | 23 |
| $A_1B_2$ | 13<br>121 | 1<br>122 | 11<br>123 | 25 |
| $A_2B_1$ | 94<br>211 | 58<br>212 | 15<br>213 | 167 |
| $A_2B_2$ | 140<br>221 | 98<br>222 | 73<br>223 | 311 |
| $A_1B^+$ | 22 | 9 | 17 | 48 |
| $A_2B^+$ | 234 | 156 | 88 | 478 |
| $A^+B_1$ | 103 | 66 | 21 | 190 |
| $A^+B_2$ | 153 | 99 | 84 | 336 |
| $A^+B^+$ | 256 | 165 | 105 | 526 |

$A_1$ = trap captures, $A_2$ = trap failures, B = $CO_2$ ($B_1$ high, $B_2$ low), C = habitat ( $C_1$ deep, $C_2$ shallow, $C_3$ rock), A+, B+, C+ - total numbers in each of those letters.

TABLE 27

Fienberg's contingency table test for aspen upland 1975-76: $\chi^2$ values

| Cell | Observed no. of captures | Model 1* Expected no. of captures | Model 1* $\chi^2$ | Model 2** Expected no. of captures | Model 2** $\chi^2$ | Model 3*** Expected no. of captures | Model 3*** $\chi^2$ | Model 4**** Expected no. of captures | Model 4**** $\chi^2$ |
|---|---|---|---|---|---|---|---|---|---|
| 111 | 9 | 8.4 | 0.0429 | 9.4 | 0.0170 | 8.9 | 0.0011 | 12.5 | 0.9800 |
| 112 | 8 | 5.4 | 1.2519 | 6.0 | 0.6667 | 3.6 | 5.3778 | 5.1 | 1.6490 |
| 113 | 6 | 3.4 | 1.9882 | 1.9 | 8.8474 | 3.4 | 1.9882 | 5.3 | 0.0924 |
| 121 | 13 | 14.9 | 0.2423 | 14.0 | 0.0714 | 13.1 | 0.0008 | 9.5 | 1.2895 |
| 122 | 1 | 9.6 | 7.7042 | 9.0 | 7.1111 | 5.4 | 3.5852 | 3.9 | 2.1564 |
| 123 | 11 | 6.1 | 3.9361 | 7.7 | 1.4143 | 13.6 | 0.4971 | 11.7 | 0.0418 |
| 211 | 94 | 83.7 | 1.2675 | 93.6 | 0.0017 | 94.1 | 0.0001 | 90.5 | 0.1354 |
| 212 | 58 | 54.0 | 0.2963 | 60.0 | 0.0667 | 62.4 | 0.3103 | 60.9 | 0.1381 |
| 213 | 15 | 34.3 | 10.8598 | 19.1 | 0.8801 | 17.6 | 0.3841 | 15.7 | 0.0312 |
| 221 | 140 | 148.0 | 0.4324 | 139.0 | 0.0072 | 139.9 | 0.0001 | 143.5 | 0.0854 |
| 222 | 98 | 95.4 | 0.0709 | 90.0 | 0.7111 | 93.6 | 0.2068 | 95.1 | 0.0884 |
| 223 | 73 | 60.7 | 2.4924 | 76.3 | 0.1427 | 70.4 | 0.0960 | 72.3 | 0.0068 |
| | | | 30.5849 (df = 8) | | 19.9374 (df = 5) | | 12.4476 (df = 3) | | 6.6944 (df = 2) |

Model 1 vs. Model 2: $\chi^2 = 10.6474$ (df = 3, p = 0.05)

Model 2 vs. Model 3: $\chi^2 = 7.4898$ (df = 2, p = 0.05)

Model 3 vs. Model 4: $\chi^2 = 5.7810$ (df = 1, p = 0.05)

*Model 1: 1 + A + B + C

**Model 2: 1 + A + B + C + BC

***Model 3: 1 + A + B + C + BC + AC

****Model 4: 1 + A + B + C + BC + AC + AB with both having significant effects on the numbers of captures but some other factor causing the significant remainder of unexplained variation ($x^2$ = 6.7, df = 2) was also present. This could have been due to "trap addict" animals, predators, nonfunctioning traps or any number of unknowns.

# DISCUSSION

## SECTION 1.

### $CO_2$ ACCUMULATION

In this study, I found a consistent variation between habitats in the accumulation of subnivean $CO_2$. This could explain why some authors found $CO_2$ accumulated (Bashenina 1956, Kelley et al 1968, and others) while others did not (Fuller and Holmes 1972, Reiners 1968, and Coyne and Kelley 1971). The $CO_2$ concentrations measured in this study agreed with those found by other authors (Coyne and Kelley 1971, Kelley et al. 1968, Bashenina 1956). Havas and Mäenpää (1972) recorded accumulations of three to four times the atmospheric levels in their area (0.028%/volume $CO_2$) while I measured maximum concentrations up to four or five times the atmospheric levels that I recorded (0.02 %/volume) at the Taiga Biological Station and the Experimental Lakes Area near Kenora, Ontario. The reduced amounts of atmospheric $CO_2$ in my study may be due to the large amount of continually green vegetation (conifers) available for photosynthesis above the snow and to the lack of air pollution in the area. The atmospheric levels recorded by Havas and Mäenpää (1972) are less than those of other authors from areas without evergreens (0.035%/volume $CO_2$, Kelley et al 1968).

I found that $CO_2$ concentrations in some areas such as the aspen upland and alder ridge ecotone showed sustained accumulations until the spring critical period and ambient mixing. In contrast $CO_2$ concentrations in the alder tamarack bog and jackpine ridge sometimes increased above ambient and then usually returned quickly to ambient concentrations. Reiners (1968), Coyne and Kelley (1971) and Kelley et al (1968) found $CO_2$ concentrations decreased to ambient levels or less once the hiemal threshold had been reached but they studied a few habitats intensively and thus may not have encountered habitats with sustained accumulations.

Kelley et al (1968) found subnivean $CO_2$ levels to be most consistent from 1000 to 1600 hours. I found that subnivean concentrat- ions of $CO_2$ changed little over a number of days and changed very little throughout the daylight hours in an area with ambient levels of subnivean $CO_2$. However, as there may have been diel variation at sites with accumulating $CO_2$, all measurements were taken between 1000 and 1600 hours.

The $CO_2$ concentrations that I found to be much lower than ambient may have been due to moss growth (Hagerup in Kalela 1962) or other plant photosynthesis that can occur at temperatures as low as $0^{o}C$. (Havas and Mäenpää 1972). This, with the light available under a snowcover of 15 cm. (Evernden 1966), could allow photosynthesis to use up subnivean $CO_2$ and create the reduced $CO_2$ concentrations. The fact that these reduced $CO_2$ levels occured only occasionally after there was thicker snow, supports this conclusion.

SECTION 2.

## FACTORS INFLUENCING $CO_2$ ACCUMULATION

The consistency of accumulation or lack of accumulation of $CO_2$ in five of six plots suggests that $CO_2$ accumulation is habitat or site-dependent. The site-dependent factors measured in this study do not uphold that assumption because neither soil depth, microtopographic change nor the amount of green vegetation contributed significantly to the predicted value of $CO_2$ concentrations. Generally, areas with deeper, well-developed soils (> 25 cm., aspen upland) exhibited the greatest $CO_2$ accumulations and greater concentrations occurred in the top 10 cm. of soil than occurred in the subnivean space. Areas with very shallow soils (≤10 cm., jackpine ridge) did not have this mass for root respiration and thus did not accumulate $CO_2$. Areas without green vegetation or soil such as bare rock in the aspen upland never accumulated $CO_2$ since there was no biological source to produce it. But, areas with little green vegetation did accumulate $CO_2$ so plant respiration is not necessarily a major producer of subnivean $CO_2$.

General site-dependent factors such as moisture may be of greater importance than I initially thought. Wet, but not saturated organic soils produce more $CO_2$ than drier ones (Polyakova 1970, Coyne and Kelley 1971). This was true in the alder ridge ecotone and aspen upland. The saturated peat of the alder tamarack bog did not accumulate $CO_2$ because there was little air space available for gas exchange and thus there was a decrease in respiration. The black spruce bog was drier than the alder tamarack bog; this might have accounted for its greater $CO_2$ concentrations.

I agreed with Van der Drift and Witkamp, (in Witkamp 1963) that pH had little effect on decomposition rates, rather than the decreased rates found by Flanagan and Scarborough (1972) when pH was outside the range 5 to 7.5. Three habitats had pH values less than 5 and two of these accumulated subnivean $CO_2$.

The presence of wind is rarely felt on the floor of the boreal forest, so that the effect of wind stated by Kelley et al (1968) was not evident.

The age and depth of litter mentioned by Reiners (1968) and Witkamp (1966) did not seem to influence $CO_2$ accumulation. The aspen upland and the alder tamarack bog had the greatest litter fall of the six habitats (deciduous versus primarily coniferous) but one had the greatest accumulation of $CO_2$ while the other had no accumulation.

The mean subnivean temperatures in the six habitats were rarely less than the critical $-7^{o}C$. that was correlated with the cessation of $CO_2$ production from decomposition (Flanagan and Scarborough 1972). The aspen upland had the warmest subnivean temperatures and the greatest $CO_2$ accumulation. The alder tamarack bog was warmer, but accumulated less $CO_2$, than the black spruce bog. Also, there was no strong correlation between $CO_2$ concentrations and subnivean temperatures while subnivean temperatures only contributed significantly to the predictive value of $CO_2$ concentrations once in one habitat during the two year study.

Of the environmental parameters measured in this study site-independent factors, particularly snow factors of hardness, density, thickness and number of ice layers, had the greatest effect on subnivean $CO_2$ accumulation in both winters. They made up over half (54%, 65%) of the significant variables contributing to the prediction of $CO_2$ concentrations in both winters while being only 4 of 15 parameters. The most important snowcover parameters were density and hardness. The relationship between these two parameters was not clear but the fact thay they affect $CO_2$ accumulations is not surprising because they characterize the blanket or container that confines the subnivean $CO_2$. Denser, harder and thicker layers of snow would impede the diffusion of $CO_2$ from the subnivean space.

The production of $CO_2$ on one habitat and the lack of it on another would reasonably depend upon the site-dependent variables in that habitat. Unfortunately this was not the case in the three site-dependent variables I measured in this study. The effect of all parameters was obscured because of the lag time from their onset to their effect on the $CO_2$ production. A controlled experiment where different factors could be removed so as to remove or control lag effects better would allow relationships to be stronger and more obvious.

SECTION 3.

## EFFECT OF $CO_2$ ON SMALL MAMMAL DISTRIBUTION

Number of small mammals captured increased from 1973 to 1976. This is especially evident in the last year of the study where more individuals were captured over the winter than had been captured the previous summer. Such an increase could have been the result of subnivean breeding (Fuller 1977) or increased juvenile survival. However, no markedly juvenile voles were captured.

*Clethrionomys gapperi* was the small mammal captured most frequently in all six habitats. Fuller (1977) also found *C. gapperi* to be the boreal small mammal captured most commonly. *Microtus pennsylvanicus* can occupy the same type of habitat as *C. gapperi* (Iverson and Turner 1972, Payne 1974, Riewe 1973) and was increasing in numbers towards the end of the study. The remaining small mammal species in the study area were captured rarely if ever in winter.

The significant decrease in numbers of captures before and after the hiemal threshold, in all cases where there were large enough numbers of captures to be significant, is related to the fall critical period or time between thermal overturn (when the ground temperatures become colder than the air temperatures) and onset of the hiemal threshold (Pruitt 1957, Fuller et al 1969). It is a time of environmental stress and small mammals without home ranges, food stores, nests or those that are not in peak physical condition are subject to its adverse effects. Many small mammals do not appear to live through a second winter (Hamilton 1942, Pernetta 1976); this would be expressed as a decreased post-snowfall capture rate (Gunderson in Stebbins 1976). The fall critical period was especially important in determining survival of small mammals in all four of the habitats trapped in winter.

The aspen upland and the alder ridge ecotone exhibited the greatest diversity of microtopography, significant $CO_2$ accumulations and significant effects of $CO_2$ ($p < .01$) on small mammal distributions. The specific movements of marked small mammals away from greater $CO_2$ concentrations and their return once the concentrations had lessened in the aspen upland, were indicative of the effect of $CO_2$ accumulations.

Small mammals respond physiologically to concentrations of $CO_2$ as low as 1 or 2% (Galantsev and Tumanov 1969) at temperatures about $20^{o}C$. and when stressed by lower temperatures they respond to amounts less than 1 or 2% (Dawson 1955, Baudinette 1974). The values I measured in the subnivean space (up to 0.12%/volume) while not as great as these were much greater than the ambient (0.02%/volume). In an enclosed subnivean area such as a nest, the $CO_2$ could accumulate to even greater levels than those I measured in the subnivean space.

The response of small mammals to increased $CO_2$, causing increased respiratory function, decreased heart rate and rectal temperatures may be an adaptive response to the stress caused by increased $CO_2$ concentrations. These altered body functions may lead to lessened activity, decreased winter metabolic rates and related lower calorie requirements. However, these adaptive responses may themselves cause problems for the animals. The lower reaction rate could lessen the small mammals' sensory preception to temperature differences, food and predators and thus decrease their survival rate. The changes in small mammal distribution that I observed were associated with increase in $CO_2$. These physiological responses to $CO_2$ could lead to the aforementioned changes in distribution. It would be advantageous for the small mammal to frequent areas which elicit less physiological stress (i.e., those with less $CO_2$).

If food shortages caused the changes in distribution shown in the aspen upland and alder ridge ecotone one would also expect marked changes in the distribution of small mammals in the alder tamarack bog. This did not happen. The standard error to mean subnivean temperatures was low in all four plots. Higher small mammal numbers are not necessarily related to available food (Gorecki and Gebczynska 1962, Chitty et al. 1968) or supplementary food (Watts 1968, Flowerdew 1972, Fairbairn 1977) or warmer subnivean temperatures (Fuller 1977). Thus these factors do not explain all the observed variations in distribution. Given the facts that subnivean $CO_2$ does accumulate, small mammals do react physiologically to $CO_2$, areas of homogeneous habitat that have increased concentrations of $CO_2$ have few small mammals, it is reasonable to conclude that small mammals avoid areas of greater $CO_2$ concentrations. $CO_2$ thus affects small mammal distribution. In the case of *Clethrionomys gapperi*, concentration of subnivean $CO_2$ must be considered as an additional dimension to its ecological niche.

# SUMMARY

## SECTION 1.

### $CO_2$ ACCUMULATION

$CO_2$ accumulated specifically and consistently in some habitats while not in others. The aspen upland, black spruce bog, jackpine sandplain and part of the alder ridge ecotone exhibited $CO_2$ accumulations. However, the extent and amount of accumulation varied between these habitats, being greatest in the aspen upland. $CO_2$ did not accumulate in the alder tamarack bog or the jackpine ridge. $CO_2$ accumulation was found to be similar in the same habitats in both winters.

## SECTION 2.

### FACTORS INFLUENCING $CO_2$ ACCUMULATION

The accumulation of $CO_2$ was affected primarily by snow characteristics. Subnivean temperature did not show a strong correlation with the predictive value of $CO_2$ accumulation. Neither microtopography nor amount of green vegetation prior to snowfall were significant predictors of $CO_2$ accumulation. The effect of weather (ambient air temperature and barometric pressure) was ambiguous. In a few cases signifícent correlations between either temperature or barometric pressure and $CO_2$ levels were found. One would expect weather factors to have similar effects in all areas, but this was not the case.

SECTION 3.

## EFFECT OF $CO_2$ ON SMALL MAMMAL DSITRIBUTION

The reduction in small mammal numbers was associated with the fall critical period. The absence of accumulation of $CO_2$ was significantly associated with the absence of change in small mammal distribution especially in the alder tamarack bog. The accumulation of $CO_2$ was significantly associated with the change in distribution of small mammals especially in the aspen upland.

Given the facts that subnivean $CO_2$ does accumulate, small mammals do react physiologically to $CO_2$, areas of homogeneous habitat that have increased concentrations of $CO_2$ have few small mammals, it is reasonable to conclude that small mammals avoid areas of greater $CO_2$ concentrations and thus subnivean $CO_2$ affects small mammal distributions.

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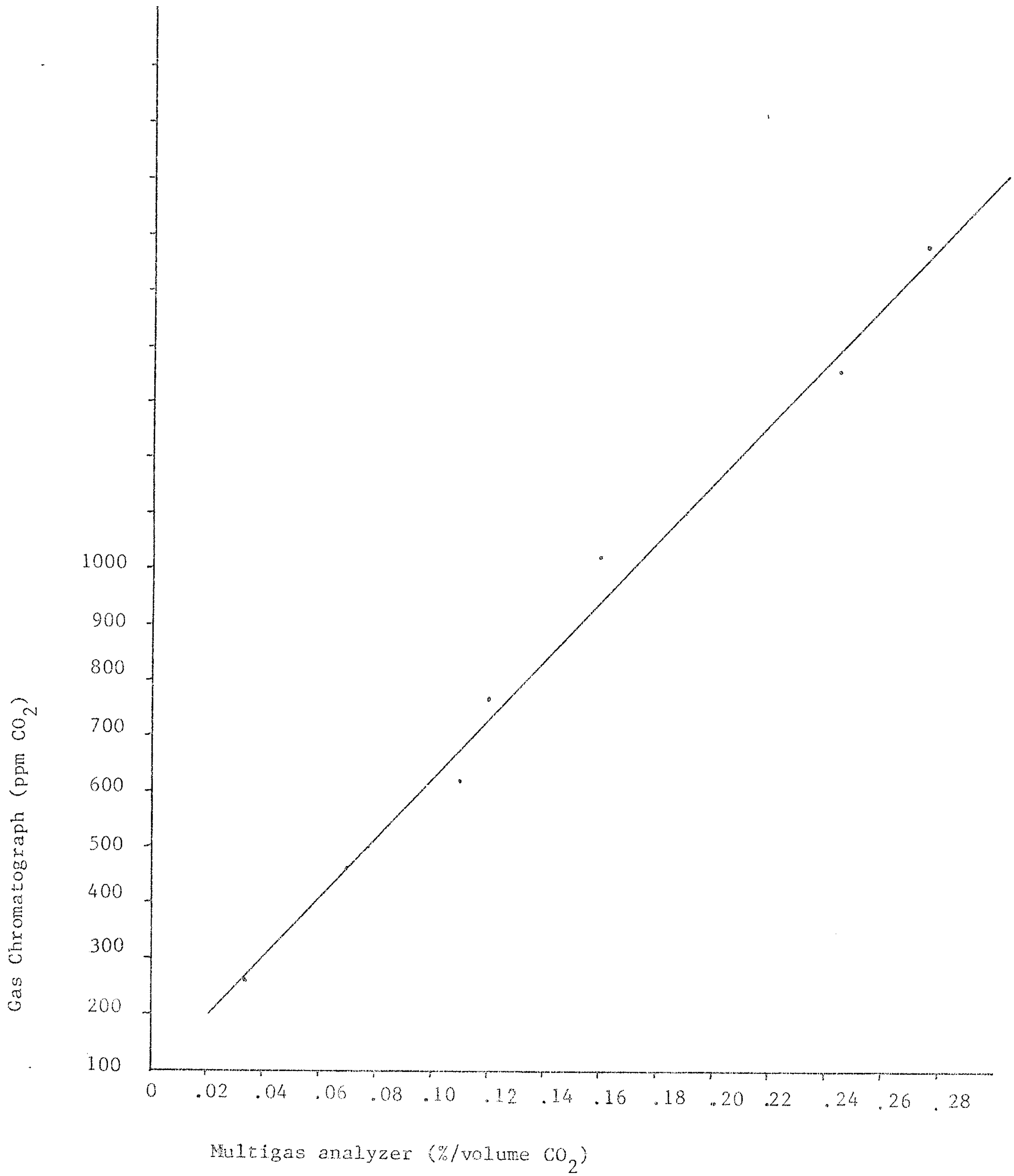
## APPENDIX A

Calibration of a Dräger multigas analyzer
against a gas chromatograph on April 3, 1974
with a_r value of 0.9956


Gas Chromatograph (ppm $CO_2$)
1000
900
800
700
600
500
400
300
200
100
0
.02
.04
.06
.08
.10
.12
.14
.16
.18
.20
.22
.24
.26
.28
Multigas analyzer (%/volume $CO_2$)

# APPENDIX B

## Procedure for Field Operation of the Dräger Multigas Analyzer

1. Keep the analyser and measuring tubes warm (with pocket warmer in paper bags or next to the body).
2. Take cork out of tygon and remove 10 pumps (approximately 5000 cc.) of air from the tube. This draws subnivean air into the tube.
3. Take meter and tube out of warm place.
4. Break ends of tube off and insert blue arrowed end into the meter, and the white end into the tygon.
5. Hold tube and tygon in bare hand to maintain as much warmth as possible. Tubes work best at about 15$^{o}$ C. and this was the quickest most efficient way of approximating this temperature. Different people measured the same reading, so this method can be used by different people for the same result.
6. Once analyzer has been pumped 10 times, remove $CO_2$ measuring tube from pump and record reading from 0 point to point when color begins to fade. Often the reading is vague, and so the reading is read from where the color begins to fade to where it has disappeared altogether (ex. .02 - .025%/volume $CO_2$). The color change was much harder to read during bright sunny light than during cloudy days.