The influence of rainfall on murid densities through a trophic chain in the Kluane boreal forest, Yukon.

by

Patrick Carrier

B.Sc., Université du Québec à Trois-Rivières, 1994

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

in

THE FACULTY OF GRADUATE STUDIES
Department of Zoology

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April 1998

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia
Vancouver, Canada

Date April 29TH 1998

DE-6 (2/88)

Abstract

Vole and mouse population densities in the Kluane boreal forest (Yukon) vary non-cyclically; densities are usually low but unpredictable and ephemeral high densities occasionally occur. Anecdotal observations suggest that vole and mouse densities could be correlated to summer rainfall amounts. Small mammal populations in Kluane are suspected to be food-limited, and food production is suspected to be rainfall-limited, since the Kluane boreal forest experiences a water-deficit during the summer.

I tested the hypothesis that rainfall acts through a trophic chain to influence vole numbers, and that vole numbers should increase with rainfall two-to-three fold as they do with addition of sunflower seed. To simulate increased rainfall, I installed irrigation systems and operated them for two summers on three areas of approximately 1.5 hectares of boreal forest habitat. I monitored small mammals, mushrooms, understory vegetation, spruce trees and forest-floor invertebrates. Three unirrigated areas of equal size were used as control grids: treatment and control grids were paired within three different sites.

Mushrooms and one species of understory plant (*Arctostaphylos uva-ursi*) responded significantly to the treatment. There was no clear treatment effect on spruce trees, invertebrates, and shrews. Voles were generally more numerous on the treatment grids than on the controls, but the difference was of the expected three-fold magnitude at only one site. Overall, only one out of three sites supported the hypothesis that vole densities can be affected by rainfall through a trophic chain.

Table of contents

Abstract ii
List of Tables v
List of Figures vi
Acknowledgments vii

Introduction 1

Methods 4
- Study area 4
- Experimental sites 5
- Irrigation pattern and schedule 6
- Sampling procedures 7
  - Fungal sporocarps 7
  - Understory vegetation biomass 9
  - Production of *Arctostaphylos uva-ursi* berries. 10
  - Spruce 11
  - Invertebrates and shrews 12
  - Rodents 13
  - Statistical analyses 14

Results 15
- Irrigation 15
- Fungal sporocarps 16
- Understory vegetation biomass 20
- Production of *Arctostaphylos uva-ursi* berries. 21
- Spruce 21
- Invertebrates and shrews 23
- Rodents 24

Discussion 28
- Fungal sporocarps 28
- Plants 30
- Invertebrates and shrews 34
- Rodents 35

Conclusion 41
Literature cited 42

Appendix I: Irrigation system design: a) grids T/1 and T/2; b) grid T/3. 45

Appendix II: Herbaceous strata plant biomasses (g dry weight) per group for all grids: 46

A) Spring and fall 1995, averages calculated using all samples. 46

B) Spring and fall 1995, averages calculated using only samples where investigated taxa were present. 46

C) Spring and fall 1995 Mann-Whitney U and p values, for averages using all samples and averages using only samples where investigated taxa were present. 46

D) Spring 1996, averages calculated using all samples. 47

E) Spring 1996, averages calculated using only samples where investigated taxa where present. 47

F) Fall 1996, averages calculated using all samples. 48

G) Fall 1996, averages calculated using only samples where investigated taxa where present. 48

H) Spring and fall 1996 Mann-Whitney U and p values, for averages using all samples and averages using only samples where investigated taxa were present. 49

Appendix III: Spring and fall 1995 A) average numbers of selected ground-dwelling invertebrates caught per trap per day on each grid B) their average biomass and C) Mann-Whitney U and p values. 50

Appendix IV: Mann-Whitney U and p values for average body weight (g) differences between treatment and control grids for *Clethrionomys rutilus* at each site for three trapping sessions. 51

List of Tables

Table 1: Precipitation (mm of rain) that fell between May and August during both experimental years, as well as average amount of water (mm) added at 2 m from each sprinkler on each treatment grid. 15

Table 2: Sample size (N), averages and standard deviations (S.D.) of total sporocarp numbers per transect for each grid for both 1995 and 1996 fall surveys. 16

Table 3: Mann-Whitney U values and probability for numbers of small, medium, large and total mushrooms for both 1995 and 1996 surveys. 16

Table 4: Sample size (N), averages and standard deviations (S.D.) of small sporocarp numbers (diam. < 4 cm) per transect for each grid for both 1995 and 1996 fall surveys. 17

Table 5: Sample size (N), averages and standard deviations (S.D.) of medium sporocarp numbers (diam. 4-8 cm) per transect for each grid for 1995 and 1996 fall surveys. . .17

Table 6: Sample size (N), averages and standard deviations (S.D.) of large sporocarp numbers (diam. > 8 cm) per transect for each grid for both 1995 and 1996 fall surveys. 18

Table 7: Average mushroom fresh biomass (g) per transect for each grid, for small- (diam. < 4 cm), medium- (diam. 4-8 cm), and large- (diam. > 8 cm) sized mushrooms, as well as for all mushrooms regardless of size (total). 19

Table 8: Mann-Whitney U values and probability for biomass of small, medium, large and total mushrooms for both 1995 and 1996 surveys. 20

Table 9: Mann-Whitney U and p values for differences in the average number and weight of *Arctostaphylos uva-ursi* berries per quadrat between treatment and control grids. . . 22

Table 10: Numbers of *Sorex cinereus*, *S. monticolus* and *Microsorex hoyi* captured per trap per day in the fall 1995 pitfall-trap invertebrate survey. 23

Table 11: Minimum number of individuals known alive per grid, for the four rodent species caught in September 1995, after the first summer of irrigation. 24

Table 12: Minimum number of individuals known alive per grid, for the four rodent species caught in June 1996, before the second summer of irrigation. 26

Table 13: Minimum number of individuals known alive per grid, for the four rodent species caught in August 1996, after the second summer of irrigation. 26

Table 14: Adult *C. rutilus* numbers (N) and average body weight (g) per grid, for three trapping sessions. 27

List of Figures

Figure 1: Average monthly water balance for Aishihik, Yukon, showing a water deficit for each of the summer months (using data from Thornthwaite, 1962). 3

Figure 2: Hypothesized influence of rainfall on murid densities through a trophic chain. 4

Figure 3: Location of the three study sites in relation to Kluane Lake, Yukon. 5

Figure 4: Average irrigation efficiency (mm of water/unit area/h) against distance (m) away from sprinklers. 6

Figure 5: White spruce (*Picea glauca*) lateral branch growth (LBG) measurements for 1994 (reference year), 1995 and 1996. 12

Figure 6: Linear relationship between individual mushroom fresh biomass (g) and its respective cap area (square mm) as calculated from 62 mushrooms collected in August 1995. 19

Figure 7: Average number of *Arctostaphylos uva-ursi* berries (1995 crop) per quadrat for the two grids on each experimental site. 22

Figure 8: Average number of *Arctostaphylos uva-ursi* berries (1996 crop) per quadrat for the two grids on each experimental site. 22

Figure 9: White spruce average lateral branch growth ratio (LBG 1995/LBG 1994) for the two grids on each experimental site. 22

Figure 10: White spruce average lateral branch growth ratio (LBG 1996/LBG 1994) for the two grids on each experimental site. 22

Figure 11: Minimum number of *C. rutilus* individuals known alive on C/1 (Diamonds) and T/1 (open circles) grids, during the 4 trapping sessions carried out throughout the entire duration of the experiments (April 1995 to September 1996). 25

Figure 12: Minimum number of *C. rutilus* individuals known alive on C/2 (Diamonds) and T/2 (open circles) grids, during the 4 trapping sessions carried out throughout the entire duration of the experiments (April 1995 to September 1996). 25

Figure 13: *C. rutilus* minimum number of individuals known alive on C/1 (Diamonds) and T/1 (open circles) grids, during the 4 trapping sessions carried out throughout the entire duration of the experiments (April 1995 to September 1996). 25

Acknowledgments

This research project was achieved thanks to suggestions and help from many people. I would like first to thank my advisor, Charles Krebs, and as well Rudy Boonstra, for the initial suggestion of the hypothesis tested in my thesis, and for ongoing helpful suggestions and advice given to me throughout this project. I would like to thank as well my committee members, Judy Myers, Jamie Smith and Roy Turkington for their useful suggestions and for reviewing this thesis. Thanks as well to David Preikshot, Karen Hodges, Dennis Chitty and Jordan Rosenfeld for reviewing my thesis. Irene Wingate, Mark O'Donoghue, Frank Doyle, Jocylyn McDowell and Andy Williams provided logistical help of vital importance, both to me and for the project itself. I am very much owing to Tina Raudzus, whose assistance with field work was invaluable. Thanks to Gillian Turney, Jan Jekielek, and numerous other people, most of them somewhat involved with the C.S.P., who helped with field work. As well, I would like to thank The Kluane Lake Base of The Arctic Institute of North America and its staff for providing me with living and research facilities. Finally, I would like to thank the three beaver families whose permanent ponds I used as sources of water, and who seemingly did not mind my use of a bit of their water. Their work was imperative to this experiment!! To all of you I say a big thanks! This project was supported by an N.S.E.R.C. and an N.S.T.P. grant to P. Carrier and by an N.S.E.R.C. operating grant to C.J. Krebs.

Introduction

In the Kluane boreal forest (Yukon), small mammal populations fluctuate in an irregular fashion (Gilbert and Krebs, 1981, 1991). Baseline population densities are usually low, but unpredictable outbreaks in numbers occur (Gilbert and Krebs, 1981, 1991). The causes for these outbreaks are not clear, but the Kluane region lies in the rain shadow of the St. Elias mountains, and summer drought could be a general factor limiting ecosystem productivity, including vole densities. Hence, increased summer rainfall which varies unpredictably from year to year could generate rodent outbreaks. Studies in a desert ecosystem (Beatley, 1969, 1976) and in an arid shrub-steppe (Dunigan *et al.*, 1980) have demonstrated the dependence of some small mammal populations on rainfall, through bottom-up trophic chains mediated by rainfall. Through experimental irrigation of boreal forest habitat, I tested the hypothesis that murid numbers in Kluane respond to a bottom-up trophic chain in relation to the amount of rainfall. Fungi, plants, and insects are predicted to respond to changes in rainfall, thereby influencing rodent population densities.

Fungal sporocarps, a potential food source for murids (Banfield, 1974), should increase in abundance with increasing rainfall (Wilkins and Patrick, 1939; Wilkins and Harris, 1946). Further, since fungi are the most important decomposers in the boreal forest (Frontier and Pichod-Viale, 1990), soil nutrient availability could change in response to changes in fungal growth as a consequence of irrigation. Primary production in the boreal forest is limited by nutrient availability (Zasada *et al.*, 1977), and therefore fungal production could influence murid densities both directly and indirectly, through greater mushroom availability and increased plant production resulting from increased nutrient availability.

Since the Kluane boreal forest lies in a rain-shadow zone (Rowe, 1972), the resulting shortage of rainfall leads to a water deficit during each month of the summer (Figure 1). Water deficits are revealed when the potential evapotranspiration (P.E.T.) is greater than the actual evapotranspiration (A.E.T.). The potential evapotranspiration is the amount of water that could be transpired by the vegetation for photosynthesis and the water that would evaporate from the soil, given that water were in sufficient quantity. The actual evapotranspiration is the quantity of water that is evaporated and transpired by plants, according to how much water is available in the soil (Thornthwaite, 1957). Water deficits are know to reduce photosynthetic activity (Boyer, 1976) and consequently, primary production. Also, primary production is thought to be limited by nitrogen availability throughout the boreal forest (Zasada *et al.*, 1977). Yet, it has been demonstrated that both decomposition rate (Meentemeyer, 1978) and nitrogen availability (Binkley *et al.*, 1994) increase with soil humidity. Hence, plant production is expected to increase not only with greater water availability for photosynthesis but also with greater nutrient availability. Since rainfall enhancement could improve plant abundance, small herbivores might proliferate.

Demographic parameters of some animals are known to be directly influenced by weather. In many insects, survival rate, speed of development and number of eggs laid per female are strongly correlated with relative humidity (Bursell, 1964). Furthermore, some insects are known to show population outbreaks as a result of bottom-up trophic chains triggered by rainfall (Clark, 1974). I therefore expect an increase in insect populations as a result of increased rainfall. In turn, murid species such as the deer mouse (*Peromyscus*

maniculatus) and the meadow vole (*Microtus pennsylvannicus*) which are partially insectivorous (Van Horne, 1982; Banfield, 1974) could be positively influenced by this increase in the availability of insects (Figure 2).

Given these considerations, I monitored murid numbers and food sources such as fungal sporocarps, understory vegetation, spruce trees and forest-floor invertebrates. I tested the hypothesis that food availability is an important factor limiting small rodent populations in Kluane. I also tested the hypothesis that murid food-limitation is significantly influenced by rainfall. I used irrigation treatments to see if that enhanced food availability for small rodents. I expect to witness population increases of approximately two to three-fold, since artificial supplementation of food results in increases of this amount (Boutin, 1990).

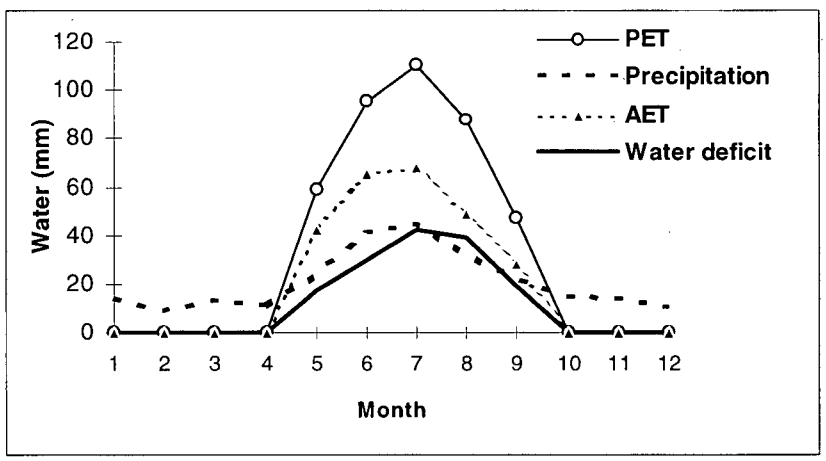


Figure 1: Average monthly water balance for Aishihik, Yukon, showing a water deficit for each of the summer months (using data from Thornthwaite, 1962). Calculation methods from Thornthwaite (1957). Soil water retention assumed to be of 150 mm. PET: potential evapotranspiration; AET: actual evapotranspiration.

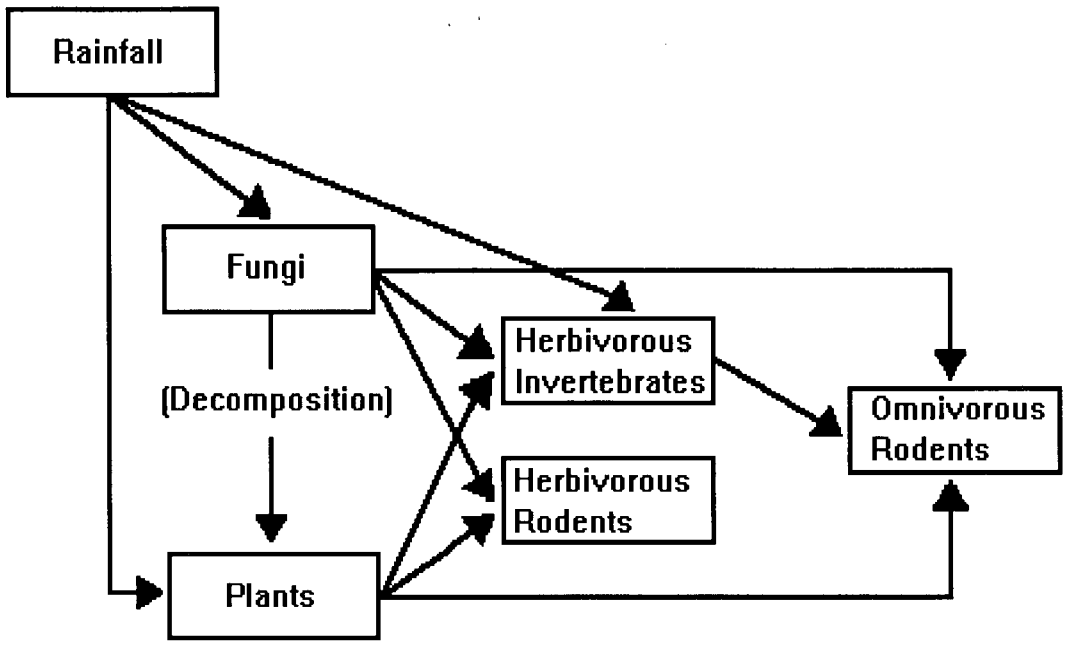


Figure 2: Hypothesized influence of rainfall on murid densities through a trophic chain.

Methods

Study area

The study area is located in the boreal forest, near Kluane Lake (61° N, 138° W), in southwestern Yukon. The study area occurs within a particular type of boreal forest, the Kluane boreal forest section (Rowe, 1972). Douglas (1974) classifies the vegetation of the locality as a *Picea glauca-Shepherdia canadensis* (closed phase) community. The area is quite dry, since it lies in the rain shadow of the St. Elias Mountains. Summer rainfall (May to August, inclusively) at Burwash Landing (on Kluane Lake) is both low and variable: it ranged from 92 to 257 mm from 1973 to 1992, averaging 181 mm, with a coefficient of variation (C.V.) of 0.223 (Environment Canada).

Experimental sites

I compared populations in irrigated (rain + irrigation; treatment) and non-irrigated (rain only; control) areas. The experiment was simultaneously replicated three times, on sites of similar vegetation types. The sites were constrained to be near ponds that could be used as water sources. The sites were separated from each other by at least three km (Figure 3). Paired treatment grids and control grids were established on each site at a distance ranging from 50 to 100 m from each other. At sites #1 and #2, the 4 square grids were staked in a 10 by 10 fashion, at regular intervals of 14 m. These 4 grids were therefore 1.6 ha in surface area. The grids on site #3 were staked at regular intervals of 14 m in a 13 by 7 fashion instead, due to topographical constraints. These latter grids were 1.4 ha in surface area.

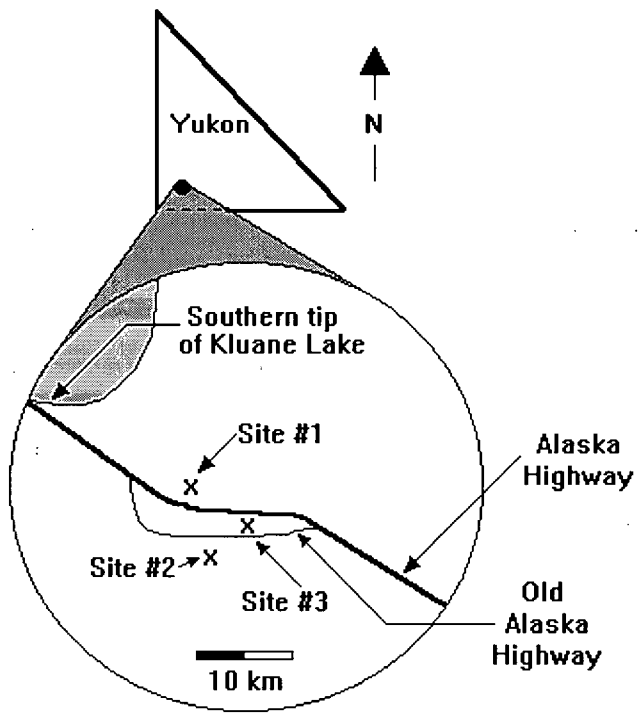


Figure 3: Location of the three study sites in relation to Kluane Lake, Yukon.

On the treatment grids, I built an irrigation system out of PVC pipes, on which rotating sprinklers (Nelson F 33s) were installed (see Appendix I). The sprinklers were 1.5 m above the ground. Water was fed to the irrigation system through the action of an 8 HP gas-powered pump (Monarch NSGF-8), which took water from a near-by pond. I did not install irrigation systems on the control grids, which were not subjected to irrigation.

Irrigation patterns and schedule

Each sprinkler had a radius of action of about 14 m, in which it delivered water at a rate of 35.8 liters/minute. Irrigation efficiency (water added per unit area) decreased with the distance from each sprinkler; maximum treatment effect was to be expected nearest the sprinkler (Figure 4). On treatment grids #1 and #2, 23 sprinklers were distributed in a checker-board fashion, while only 17 were installed on treatment grid #3 (Appendix I). On all treatment grids, sprinklers were 30 m apart. No more than 5 sprinklers were operated at once, as the pump could not supply enough water pressure to operate more.

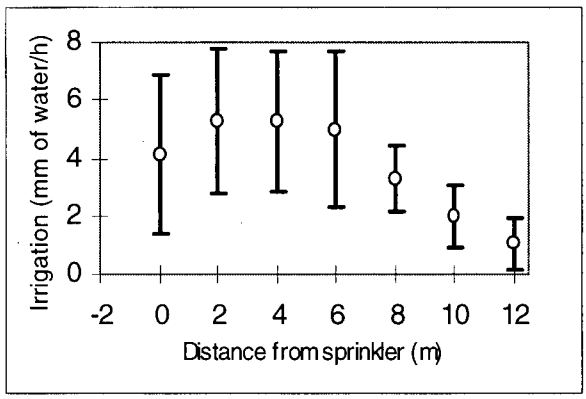


Figure 4: Average irrigation efficiency (mm of water/unit area/h) against distance (m) away from sprinklers. Error bars: Std. Dev.

The amount of water added through irrigation was estimated within 12 m range of every sprinkler (Figure 4). Rain gauges were installed at 2 m intervals along the radius of each sprinkler. Sprinklers were thereafter operated for 30 minutes and the water collected in the rain gauges was weighed to the nearest 0.01g. Mass of water collected was used to calculate the amount of water added per unit area at 2 m intervals. Measurements were then used to estimate the total amount of water added per minute. It was therefore possible to estimate the total amount of water distributed during irrigation.

In 1995, the mean amount of water added at each sprinkler was estimated to be 17 200 L, while it was estimated to be 19 900 L in 1996. Each summer, irrigation was done in three pulses. In order to estimate the difference in the watering regime between control and treatment grids, rainfall input to the control grid was assumed to be the same as the rainfall at Burwash Landing. Rainfall data came from Environment Canada.

Sampling procedures

Fungal sporocarp numbers

Sporocarps (mushrooms) were counted on each grid in 1995 and 1996, in late August when sporocarps were most numerous. Mushrooms were counted on quadrats laid in a checker-board pattern between adjacent grid stakes. During the fall of 1995, 25 quadrats of 14x2 m were used on all grids. The cap diameter of each mushroom was measured to the nearest 0.5 cm with calipers and included in one of three size classes, regardless of developmental stage: 1) small (< 4 cm); 2) medium (4-8 cm); and 3) large (> 8 cm).

For the 1996 sampling season, two quadrats per sprinkler were laid, one on either side of the sprinkler. This change in the sampling pattern was to ensure that the sampled areas on the treatment grids had experienced a standard and maximal treatment effect. The spatial distribution of quadrats on the control grids, mimicked the position of the corresponding quadrats on the treatment grids, using grid stakes as landmarks instead of sprinklers. In 1996, the quadrats measured 10x2 m. The diameter of all mushrooms encountered in 1996 was measured to the nearest 0.5 cm, regardless of developmental stage.

Fungal sporocarp biomass

Sixty-two mature mushrooms collected both off-grid and on-grid in August 1995 were used to determine the relationship between cap diameter and fresh biomass, regardless of species. The cap diameter of those mushrooms was measured to the nearest 1 mm with calipers before collection and mushrooms were individually weighed to the nearest 0.001g within a few hours after collection. The sporocarp fresh biomass per transect in 1995 was estimated using the fresh biomass to diameter relationship and the mid-class diameters for small (2 cm) and medium (6 cm) mushrooms, assuming that the mid-class values were representative of the average value of the size classes. For the large mushrooms, biomass was estimated using the minimum diameter (8 cm), hence estimating their minimal fresh biomass, as it was impossible to estimate the mid-class value. For the 1996 mushroom survey, fresh biomass of all individual mushrooms was calculated using the fresh biomass to diameter relationship according to their individual size, since all mushrooms were measured that year.

Understory vegetation biomass

Clip-plots were done in early July and mid August 1995 to estimate the above-ground biomass of the understory vegetation. On all grids in 1995, 20x20 cm clip-plot stations were distributed in a checker-board pattern relative to the grid stakes. In July, 30 samples per grid were taken 1 m to the right of grid stakes, while 30 others were taken to the left in August. This sampling pattern was used to avoid sampling the same area twice at different times. Samples from 1995 were air-dried for 3-5 months, sorted and weighed to the nearest 0.001g in three categories: 1) *Arctostaphylos uva-ursi*, 2) *Linnaea borealis*, and 3) all others. Furthermore, the summed biomasses of categories 2 and 3 was considered as the biomass of herbaceous plants, and the sum of all categories was used as the total biomass of the understory vegetation.

As the objective of this study was to compare production in the above-mentioned categories between grids, the data were analyzed in two different ways. First, data were analyzed independently for each group using all samples, regardless of the absence of some categories in the samples. Secondly, data were analyzed independently for each category, this time excluding samples where the group under investigation was totally absent. This strategy was used because understory plants in Kluane reproduce almost exclusively through vegetative reproduction, and hence do not disperse very fast (Roy Turkington, personal communication). Since the vegetation was very patchy, many samples did not contain one or more of the three groups, and therefore those samples could not be used to verify growth when the group under investigation was simply absent.

The sampling pattern of 1995 was modified in 1996 so that all clip-plots were 2 m away from sprinklers on treatment grids. The spatial distribution of the clip-plots on the control grids that year mimicked the position of the corresponding clip-plots on the treatment grids, again using particular grid stakes as landmarks instead of sprinklers. The clip-plots were larger in 1996 (30x30 cm) than in 1995. In early June 1996, the samples were taken 2 m to the right of the sprinklers on treatment grids (or the corresponding grid stake on control grids) while at the end of August they were taken 2 m to the left. This was again to ensure that clipping was only done once on a given area. Samples from 1996 were oven-dried at 60 degrees Celsius for at least 4 days in order to allow for complete drying. Samples were thereafter sorted into 10 groups (grasses, *Arctostaphylos uva-ursi* without fruit, *A. uva-ursi* fruit only, *A. rubra* without fruit, *A. rubra* fruit only, *Linnaea borealis*, *Equisetum* spp., *Epilobium* spp., *Achillea millefolium*, and all others as a group) and weighed to the nearest 0.001g. The summed biomasses of all groups but *A. uva-ursi* and *A. rubra* was considered as total herbaceous plant biomass, while the sum of all groups was considered the biomass of the entire understory vegetation. As specified for the 1995 understory vegetation biomass, the 1996 analyses were first done using all samples, secondly using only non-zero samples.

Production of *Arctostaphylos uva-ursi* berries

In July 1996, 15 permanent quadrats of 30x30 cm were installed on each grid. All berries of *A. uva-ursi* were removed, as they were berries from 1995 and possibly previous years. Each quadrat was installed as near as possible to a sprinkler, in as dense as possible a patch of *A. uva-ursi*. This was to ensure that sampled areas experienced the maximal

treatment effect and that vegetation cover would be as constant as possible. Percent cover of *A. uva-ursi* within the quadrats and the distance between quadrat and sprinkler were noted. Fruits produced during the summer of 1996 were harvested at the end of August. Fruit from each quadrat were collected, oven-dried for at least 4 days at 60 degrees Celsius, counted and weighed to the nearest 0.001g.

Spruce

White spruce (*Picea glauca*) production was estimated near the end of the 1996 growth season (early August 1996) through the "relative lateral branch growth technique" (Krebs, unpublished). This technique consists of measuring the lateral branch terminal growth (LBG) in each tree (Figure 5). Since different trees can have inherently different branch growth rates, the LBG measurement in a given tree during the experimental years is compared to the LBG of the same branch prior to the beginning of the experiment (reference year). Therefore, the resulting LBG ratio (e.g.: LBG 1996/LBG 1994) gives an index of tree growth performance during a given year as compared to the baseline reference year. The reference year used in this study was 1994, *i.e.* the growth year before the start of the experiment.

Only the trees closest to sprinklers were chosen for sampling. On the control grids, stakes in comparable positions to the sprinklers of the treatment grids were used as reference points for spruce measurements. Two to four trees per station were measured, and their relative LBG was averaged for each sampling station. For each tree selected, both circumference and distance from a sprinkler (or stake) were recorded to the nearest 1 cm

using a measuring tape. Trees less than 18 cm in circumference were excluded from the sample. Since the LBG varies between branches within any given tree (Krebs, unpublished), standards were set as to which branch to measure. The standard branch was the longest unbrowsed one at breast-height, pointing towards the sprinkler (or stake). In selected branches of selected trees, LBG from 1994 to 1996 was measured to the nearest 0.5 mm.

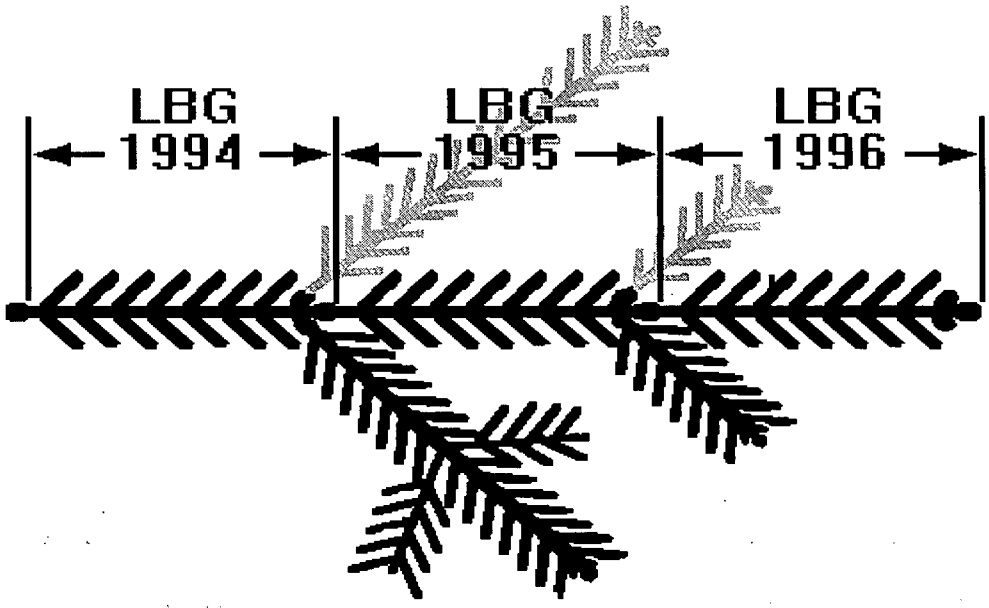


Figure 5: White spruce (*Picea glauca*) lateral branch growth (LBG) measurements for 1994 (reference year), 1995 and 1996.

Invertebrates and shrews

Population indices for forest-floor invertebrates were determined using pitfall traps. In early June 1995, 25 traps of 9 cm diameter and 12 cm depth were set at grid stakes on each grid, in a checker-board pattern. Trapping periods lasted between 10 and 26 days; the contents of the traps were stored in 70% ethanol and identified later. Pitfall traps were filled with 3 cm of water and liquid soap. The contents from traps which were disturbed by animals

or that dried-up during the trapping periods were not included in the analyses. The different taxonomic groups monitored were: land snails (Mollusca; Gastropoda), centipedes (Chilopoda), spiders (Arachnida; Araneida), grasshoppers and allies (Insecta; Orthoptera), leafhoppers (Insecta; Cicadellidae), ground beetles (Insecta; Carabidae), and carrion beetles (Insecta; Silphidae). Hymenopteran and Lepidopteran caterpillars were also monitored, and were grouped together. Other invertebrates were ignored because they were too rare. All samples were oven-dried at 60 degrees Celsius for 2-3 days, and all groups except snails, centipedes, grasshoppers and carrion beetles were weighed to the nearest 0.0001g. I thereafter calculated the number of individuals and mass (if weighed) of each group per pitfall per day. Shrews (Insectivora; Soricidae) were also captured in the pitfall traps; they were counted and identified using a key to insectivora (van Zyll de Jong, 1983). Number of shrews per trap per day were calculated for each species of shrew.

Rodents

Small rodents were live-trapped on each grid, using 50 Longworth traps per grid set at every other grid stake in a checker-board pattern. All traps were set in appropriate micro-habitats for small mammals, within 3 m of given grid stakes. Traps were prebaited (with apple bits and oats) for two days prior to trapping sessions, which lasted 2.5 days. The nest boxes of the traps were provided with "raw" cotton for rodent comfort. During trapping sessions, traps were visited once in the morning and once early at night. Captured animals were individually identified to species-level, ear-tagged, weighed (with a Pesola scale, + or - 0.5g), sexed and reproductive condition was determined before release. In females, reproductive

condition consisted of determining if individuals: 1) had recently mated (vagina opening perforated or not); 2) were lactating; and 3) were near parturition (wide gap between pubic symphyses). Obviously pregnant females were also noted. In males, determination of reproductive condition consisted of observing whether testes were scrotal or abdominal. Rodents were trapped twice a year; once in spring and once in fall, in order to get seasonal population indices. The minimum number of individuals known alive (Krebs, 1966) was used as the population index on grids.

Statistical analyses

When samples did not severely depart from the assumptions of ANOVA, nested-ANOVA tests were performed. The underlying assumptions behind ANOVAs are that the samples are of equal variances and normally distributed (Zar, 1984). Normality of the distributions was verified using histograms with data divided into approximately 10 classes. Variances of the sub-samples were compared as well. Although ANOVAs are robust to the departure from the two underlying assumptions (Zar, 1984), a non-parametric Kruskal-Wallis test was used instead of an ANOVA when the data and log-transformed severely departed from the assumptions, which was usually the case. In all cases, the statistical analyses were performed using Systat 5.1 for Windows (1990).

Results

Irrigation

During the first growing season with irrigation (1995), the total amount of rain that fell at Burwash Landing from May to August was 188 mm, whereas it was 154 mm in 1996 (Table 1). These values are respectively 104% and 85% of normal rainfall for Burwash Landing. Compared to the control grids, the treatment grids received at least 28 and 34% more water through irrigation (at 2 m distance from sprinklers) in 1995 and 1996, respectively. Those irrigation levels were between 80 and 97% (averaging 91%) of the maximal rainfall (257 mm) measured by Environment Canada in the area during 1973 to 1992.

Table 1: Precipitation (mm of rain) that fell between May and August during both experimental years, as well as average amount of water (mm) added at 2 m from each sprinkler on each treatment grid. The % increase is site-specific (e.g.:T/1 (*vs.*) C/1). Treatment grids in bold. Rainfall data from Environment Canada.

Grid	19 95				19 96			
	rain (mm)	irrigation (mm)	total (mm)	percent increase	rain (mm)	irrigation (mm)	total (mm)	percent increase
C/1	188	0	188		154	0	154	
T/1	**188**	**52**	**240**	**28**	**154**	**52**	**206**	**34**
C/2	188	0	188		154	0	154	
T/2	**188**	**62**	**250**	**33**	**154**	**74**	**228**	**48**
C/3	188	0	188		154	0	154	
T/3	**188**	**56**	**244**	**30**	**154**	**74**	**228**	**48**

Fungal sporocarp numbers

For annual mushroom surveys, the average number of mushrooms (regardless of mushroom size) per transect was higher for irrigated grids than for control grids (Table 2). This difference was significant for both years (Table 3; p = 0.05). When subdivided into three size categories (Tables 4 to 6), small- and medium-sized mushrooms were significantly more abundant on the irrigated grids for both years (Table 3; p = 0.05). Large mushrooms showed no significant difference in numbers.

Table 2: Quadrat number (N), average numbers and S.D. of total sporocarps per transect for each grid for both 1995 and 1996 fall surveys. Treatment grids in bold.

YEAR	GRID	N	AVERAGE	S.D.
	C/1	28	1.1	4.2
	T/1	**28**	**4.6**	**7.4**
1995	C/2	25	1.7	4.8
	T/2	**25**	**3.6**	**5.1**
	C/3	25	0.6	1.8
	T/3	**25**	**2.4**	**5.1**
	C/1	46	4.3	6.5
	T/1	**45**	**14.8**	**17.0**
1996	C/2	46	5.7	7.7
	T/2	**46**	**8.9**	**9.0**
	C/3	34	5.2	3.7
	T/3	**34**	**7.5**	**6.0**

Table 3: Mann-Whitney U values and probability for numbers of small, medium, large and total mushrooms for both 1995 and 1996 surveys.

YEAR	CATEGORY	U	p
	small	0.000	0.05
	medium	0.000	0.05
1995	large	2.500	0.38
	total	0.000	0.05
	small	0.000	0.05
	medium	0.000	0.05
1996	large	4.500	1.00
	total	0.000	0.05

Table 4: Sample size (N), average numbers and S.D. of small sporocarps (diameter < 4 cm) per transect for each grid for both 1995 and 1996 fall surveys. Treatment grids in bold.

YEAR	GRID	N	AVERAGE	S.D.
	C/1	28	0.9	4.1
	T/1	**28**	**1.6**	**1.9**
1995	C/2	25	0.9	2.7
	T/2	**25**	**1.7**	**3.5**
	C/3	25	0.4	1.3
	T/3	**25**	**1.8**	**4.5**
	C/1	46	3.5	6.1
	T/1	**45**	**12.6**	**15.2**
1996	C/2	46	4.0	4.3
	T/2	**46**	**6.1**	**6.6**
	C/3	34	4.1	3.5
	T/3	**34**	**5.8**	**5.0**

Table 5: Sample size (N), average numbers and S.D. of medium sporocarps (diameter 4-8 cm) per transect for each grid for both 1995 and 1996 fall surveys. Treatment grids in bold.

YEAR	GRID	N	AVERAGE	S.D.
	C/1	28	0.2	0.7
	T/1	**28**	**1.7**	**4.1**
1995	C/2	25	0.6	1.7
	T/2	**25**	**1.5**	**1.9**
	C/3	25	0.2	0.6
	T/3	**25**	**0.6**	**1.8**
	C/1	46	0.7	1.0
	T/1	**45**	**1.9**	**2.8**
1996	C/2	46	1.4	3.6
	T/2	**46**	**1.7**	**2.6**
	C/3	34	1.0	1.0
	T/3	**34**	**1.5**	**2.0**

Table 6: Sample size (N), average numbers and S.D. of large sporocarps (diameter > 8 cm) per transect for each grid for both 1995 and 1996 fall surveys. Treatment grids in bold.

YEAR	GRID	N	AVERAGE	S.D.
	C/1	28	0.0	0.2
	T/1	**28**	**1.4**	**3.3**
1995	C/2	25	0.3	0.8
	T/2	**25**	**0.5**	**0.8**
	C/3	25	0.0	0.0
	T/3	**25**	**0.0**	**0.0**
	C/1	46	0.0	0.1
	T/1	**45**	**0.0**	**0.1**
1996	C/2	46	0.2	0.8
	T/2	**46**	**0.2**	**0.6**
	C/3	34	0.1	0.3
	T/3	**34**	**0.0**	**0.2**

Mushroom biomass

The fresh biomass of individual mushrooms was correlated with their respective cap area ($R^2 = 0.93$: Figure 6). The regression equation obtained from this relationship was used to calculate mushroom fresh biomass per transect. For both study years, the overall mushroom biomass per transect was higher on the treatment grids than on the controls (Table 7), but was significant at the 0.05 level only in 1996 (Table 8).

When subdivided into three size classes, the average mushroom biomass per transect was always higher on the treatment grids than on their respective controls, except for large-sized mushrooms (Table 7). Small mushroom biomass per transect was significantly higher (Table 8; $p = 0.05$) on the treatment grids in both study years, whereas the biomass of medium-sized mushrooms was significantly higher only in 1995.

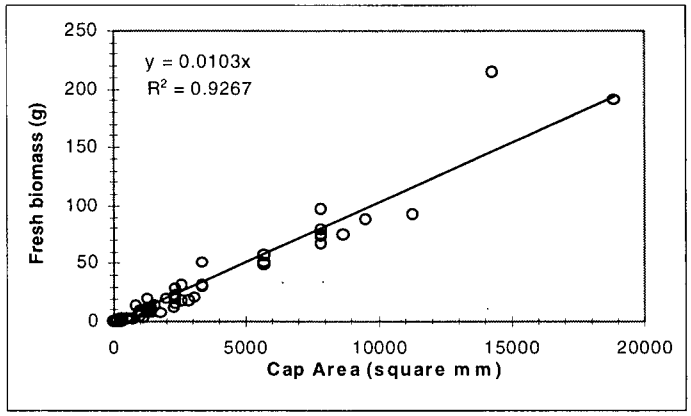


Figure 6: Linear relationship between individual mushroom fresh biomass (g) and its respective cap area (square mm) as calculated from 62 mushrooms collected in August 1995.

Table 7: Average mushroom fresh biomass (g) per transect for each grid, for small- (diameter < 4 cm), medium- (diameter 4-8 cm), and large- (diameter > 8 cm) sized mushrooms, as well as for all mushrooms regardless of size (total). Individual biomass calculated from equation shown in Figure 6. Treatment grids in bold. Sample sizes as in Table 6.

YEAR	GRID	SMALL	MEDIUM	LARGE	TOTAL
	C/1	3.1	5.6	2.0	10.8
	T/1	**5.6**	**53.1**	**76.3**	**135.0**
1995	C/2	3.1	17.7	15.7	36.5
	T/2	**5.9**	**46.8**	**27.0**	**79.7**
	C/3	1.4	5.1	0.0	6.5
	T/3	**6.3**	**19.0**	**0.0**	**25.3**
	C/1	15.8	13.6	6.7	35.4
	T/1	**47.6**	**37.0**	**1.2**	**86.3**
1996	C/2	18.3	30.6	13.2	64.3
	T/2	**27.0**	**37.4**	**15.0**	**80.8**
	C/3	22.1	21.1	5.6	49.1
	T/3	**30.9**	**27.1**	**1.5**	**64.8**

Table 8: Mann-Whitney U values and probability for biomass of small, medium, large and total mushrooms for both 1995 and 1996 surveys.

YEAR	CATEGORY	U	p
1995	small	0.000	0.05
	medium	0.000	0.05
	large	2.500	0.38
	total	1.000	0.13
1996	small	0.000	0.05
	medium	1.000	0.13
	large	6.000	0.51
	total	0.000	0.05

Understory vegetation biomass

Spring 1995

Prior to the beginning of the irrigation experiments (May 1995), the average biomass of all groups (*Arctostaphylos uva-ursi*, *Linnaea borealis*, unidentified herbaceous plants ("others"), all herbaceous plants, and all understory plants) were similar between the treatment grids and the controls (see Appendix II for averages, U and p-values). However, when excluding the null values from the analyses, *Linnaea borealis* had greater average mass per non-zero transect on the control grids (Appendix II: U = 9.000, p = 0.05).

Fall 1995

After the first summer of irrigation, the average biomass per grid of most groups remained comparable between the treatment grids and the control grids, except for the plant category of "other herbaceous plants". The latter had a significantly greater average biomass on the controls, when considering all clip-plots (Appendix II). However, no difference could be seen when considering the average biomass for non-zero transects.

Spring and Fall 1996

Prior to the resumption of irrigation in spring 1996, no difference were found in the understory plants, for all groups individually monitored that year, nor for total biomass of the understory vegetation (Appendix II). However, after the growing season that year (and irrigation), the total biomass, fruit number and the fruit biomass of *Arctostaphylos uva-ursi* per clip-plot were significantly greater on the treatment grids than on the controls (Appendix II: $U = 0.000$, $p = 0.05$). *Linnaea borealis* had greater biomass per transect on the control grids than on the treatment grids when null values were excluded.

Arctostaphylos uva-ursi berry production

The average number and weight of *A. uva-ursi* berries produced per permanent quadrat in 1995 (and possibly previous years) show no trend according to treatment (Figure 7 and Table 9: $U = 5.000$, $p = 0.83$). In 1996 (Figure 8), berry numbers per permanent quadrat were higher on all treatment grids than on the controls. Unlike the results from the clip-plots, these differences were not statistically different (Table 9: $U = 2.000$, $p = 0.27$).

Spruce lateral branch growth

A nested ANOVA was used to compare white spruce branch growth for 1995 and 1996 relative to 1994 since the data did not depart significantly from ANOVA assumptions. Overall, relative branch growth did not significantly increase in response to the treatment (Figures 7 and 8), either in 1995 (F-ratio=0.01, $p>0.25$), or in 1996 (F-ratio=1.9, $p>0.10$).

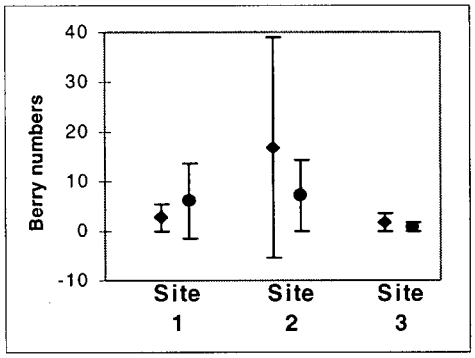


Figure 7: Average number and Std. Dev. of *A. uva-ursi* berries (1995 crop) per quadrat for the two grids on each experimental sites. Diamonds: controls; circles: treatments. Sample size of 15 quadrats/grid.

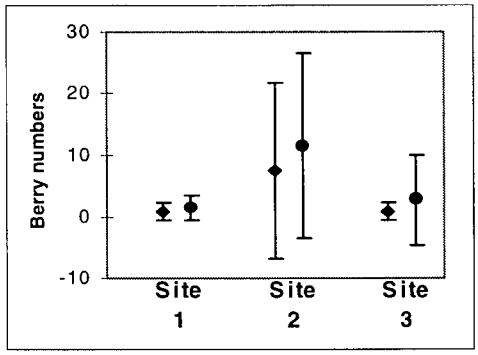


Figure 8: Average number and Std. Dev. of *A. uva-ursi* berries (1996 crop) per quadrat for the two grids on each experimental sites. Diamonds: controls; circles: treatments. Sample size of 15 quadrats/grid.

Table 9: Mann-Whitney U and p values for differences in the average number and weight of *Arctostaphylos uva-ursi* berries per quadrat between treatment and control grids.

YEAR	PARAMETER	U	p
1995	Number	5.000	0.827
	Weight (g)	5.000	0.827
1996	Number	2.000	0.268
	Weight (g)	2.000	0.275

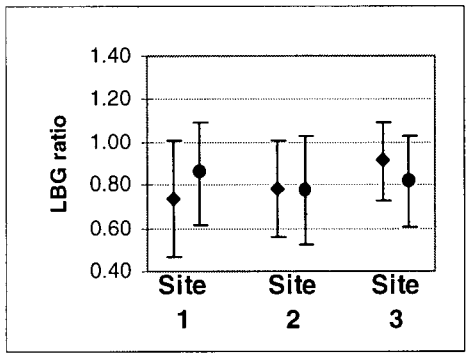


Figure 9: White spruce average lateral branch growth ratio (1995/1994) for the two grids on each site. Diamonds: controls; circles: treatments. Error bars: Std. Dev. Sample sizes of 46 (sites#1 and #2) and 37 (site #3)trees/grid.

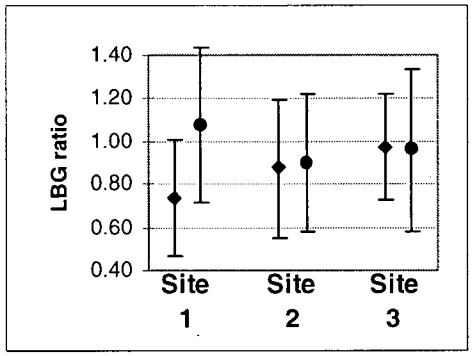


Figure 10: White spruce average lateral branch growth ratio (1996/1994) for the two grids on each site. Diamonds: controls; circles: treatments. Error bars: Std. Dev. Sample sizes of 46 (sites#1 and #2) and 37 (site #3)trees/grid.

Invertebrates and shrews

Prior to the start of the irrigation experiment in June 1995, no significant difference was found in invertebrate numbers (see Appendix III). Ground beetles, however, had a significantly higher biomass on the treatment grids (Appendix III). In the fall survey after the first summer of irrigation, only centipedes and lepidopteran caterpillars seemed to have responded significantly to the treatment by a reduction in numbers on the treatment grids as compared to the controls (Appendix III: U = 9.000, p = 0.05).

Three species of shrews were found in the pitfall samples: *Sorex cinereus*, *S. monticolus* and *Microsorex hoyi*. Few animals were caught in spring 1995 (total of 23 for the 6 grids), while in the fall of the same year, they were found in greater numbers (total of 146). Of these three species, only *S. monticolus* showed a consistent difference in number of animals captured per trap per day after the first summer of irrigation. This species was found in greater numbers on the treatment grids than on the controls, with the difference ranging from 30 to 80% (Table 10). However, this difference was not statistically significant (Table 10: U = 2.000, p = 0.28).

Table 10: Numbers of *Sorex cinereus*, *S. monticolus* and *Microsorex hoyi* captured per trap per day in the fall 1995 pitfall-trap invertebrate survey, during 26 (sites #1 and #3) and 19 (site #2) trap/days. Treatment grids in bold. Mann-Whitney U values and probability shown on right hand side of the table.

Species	C/1	**T/1**	C/2	**T/2**	C/3	**T/3**	U	p
S. cinereus	0.045	**0.023**	0.008	**0.035**	0.023	**0.023**	4.000	0.82
S. monticolus	0.014	**0.020**	0.006	**0.011**	0.012	**0.016**	2.000	0.28
M. hoyi	0.002	**0.012**	0.003	**0.007**	0.012	**0.007**	2.500	0.37
TOTAL	0.061	**0.055**	0.017	**0.053**	0.046	**0.045**	4.000	0.83

Rodents

Population densities

Prior to the start of the irrigation experiments (Spring 1995), no murid rodents were caught on any of the 6 grids; however, some least chipmunks (*Eutamias minimus*) were caught at site #3, but were neither marked nor counted. Small mammal populations were generally low and variable during the entire duration of the experiment, hence the difficulty of statistical analyses. Further, not enough data was available to analyze sex-ratio and reproductive conditions.

By the end of the first experimental year, at least three species of murids were present on some grids (Table 11). *Clethrionomys rutilus* (boreal red-backed vole) was the most commonly caught species on all grids (Table 11). At the end of the first experimental year, boreal red-backed voles were found in greater numbers on the treatment grids than on the controls, except at site #2 were they were in equal numbers (Table 11 and Figures 11 to 13). However, these differences in numbers have little biological significance, given the overall very low population densities. The other rodent species were only occasionally caught or were restricted to a particular site (Tables 11 to 13). Therefore, interpreting of their population densities is impossible.

Table 11: Minimum number of individuals known alive per grid (both juveniles and adults), for the four rodent species caught in September 1995, using fifty traps per grid for 3trap/nights. Treatment grids in bold.

Species	C/1	**T/1**	C/2	**T/2**	C/3	**T/3**
Clethrionomys rutilus	1	**2**	2	**2**	0	**3**
Peromyscus maniculatus	0	**0**	0	**0**	3	**4**
Microtus spp.	1	**0**	0	**0**	0	**1**
Eutamias minimus	0	**0**	0	**0**	2	**7**

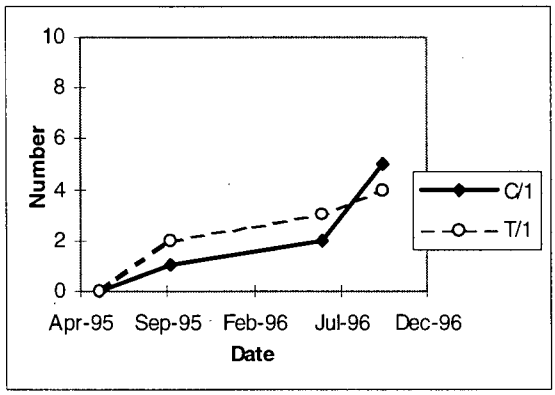


Figure 11: *C. rutilus* minimum number of individuals known alive (both juveniles and adults) on C/1 (diamonds) and T/1 (open circles) grids, during the 4 trapping sessions (April 1995 to September 1996). Fifty traps per grid were set for 3 trap/nights during each session.

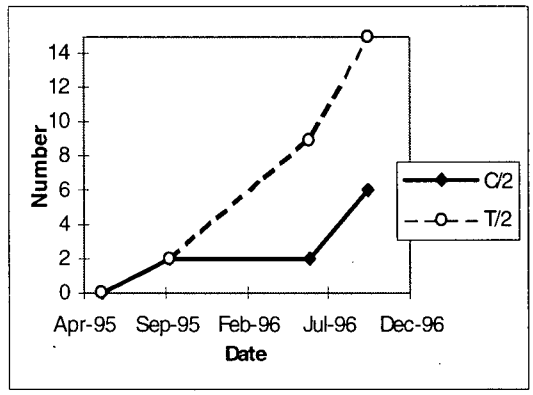


Figure 12: *C. rutilus* minimum number of individuals known alive (both juveniles and adults) on C/2 (diamonds) and T/2 (open circles) grids, during the 4 trapping sessions (April 1995 to September 1996). Fifty traps per grid were set for 3 trap/nights during each session.

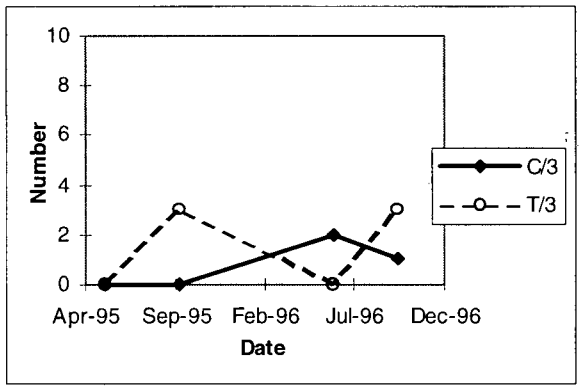


Figure 13: *C. rutilus* minimum number of individuals known alive (both juveniles and adults) on C/3 (diamonds) and T/3 (open circles) grids, during the 4 trapping sessions (April 1995 to September 1996). Fifty traps per grid were set for 3trap/nights during each session.

Table 12: Minimum number of individuals known alive per grid (both juveniles and adults), for the four rodent species caught in June 1996, using fifty traps per grid for 3trap/nights. Treatment grids in bold.

Species	C/1	**T/1**	C/2	**T/2**	C/3	**T/3**
Clethrionomys rutilus	2	**3**	2	**9**	2	**0**
Peromyscus maniculatus	0	**0**	0	**0**	2	**2**
Microtus spp.	0	**0**	1	**0**	0	**0**
Eutamias minimus	0	**0**	0	**0**	7	**7**

Table 13: Minimum number of individuals known alive per grid (both juveniles and adults), for the four rodent species caught in August 1996, using fifty traps per grid for 3trap/nights. Treatment grids in bold.

Species	C/1	**T/1**	C/2	**T/2**	C/3	**T/3**
Clethrionomys rutilus	5	**4**	6	**15**	1	**3**
Peromyscus maniculatus	0	**0**	0	**1**	6	**2**
Microtus spp.	1	**0**	2	**1**	0	**2**
Eutamias minimus	0	**0**	0	**0**	10	**8**

When the irrigation experiments were resumed in spring 1996, populations of *C. rutilus* were generally larger than during the preceding fall (Table 12 and Figures 11 to 13) indicating immigration or breeding in late autumn or early spring. The differences between the irrigated grids and their respective controls were no longer consistent across all sites, as the control grid at site #3 had three animals while its respective treatment grid had none. However, on the other two sites, more individuals were caught on the treatment grids than on the controls (Table 12 and Figures 11-12). As in the previous trapping session, the difference between C/1 and T/1 was small; conversely, the contrast between C/2 and T/2 was substantial. By the end of the second year of irrigation (August 1996), only T/2 had a substantially greater

number of boreal red-backed voles than its respective control grid; site #3 showed a similar trend (the difference was not as substantial) and site #1 showed a slight (but insignificant) opposite trend (Table 13 and Figures 11 to 13).

Overall, a greater number of *C. rutilus* were found on treatment grids than on their respective controls, for six site-trapping sessions out of nine (Figures 11 to 13). In only one case were there the same number of animals on both grids on a site (T/2 and C/2, September 1995), while in two cases there were more animals on a control grid than on its paired treatment grid.

Adult body weight

When present on both a treatment grid and its respective control, *C. rutilus* had a greater average adult body weight on the treatment grids than on the controls, in three out of four cases (Table 14). The exception occurred in fall 1996, when the average body weight of animals on C/1 grid was higher than on T/1. Those differences were not statistically different, although they came close to being so in spring 1996 for C/1 compared to T/1 (Appendix IV: $U = 0.000$, $p = 0.08$). Reproductive status also showed no trend.

Table 14: Adult *C. rutilus* numbers (N) and average body weight (g) per grid, for three trapping sessions. When no animals were present, average body weight was considered non-applicable (n/a). Treatment grids in bold.

Trapping Session	C/1		**T/1**		C/2		**T/2**		C/3		**T/3**	
	N	Mass(g)	N	Mass(g)	N	Mass(g)	N	Mass(g)	N	Mass(g)	N	Mass(g)
Fall 1995	0	n/a	**1**	**24.0**	0	n/a	**1**	**23.5**	0	n/a	**0**	**n/a**
Spring 1996	2	26.3	**3**	**27.2**	2	22.8	**7**	**24.3**	2	22.0	**0**	**n/a**
Fall 1996	3	22.5	**2**	**21.5**	3	23.3	**5**	**25.9**	0	n/a	**1**	**24.0**

Discussion

This study measured the responses of several trophic levels to a simulated increase in rainfall as a test of community responses to variations in weather conditions. The responses varied with respect to the group of organisms under investigation. I first discuss the trends found in each trophic level or functional group and experimental discrepancies. I then discuss the status of the trophic chain model proposed in the introduction.

Mushrooms

Mushroom numbers

Of all the parameters examined in this study, total mushroom numbers responded most strongly to the treatment (Tables 2 and 3). The general dependence of mushroom production on rainfall is well recognized: "Environmental conditions, particularly rainfall and temperature, have a marked effect on the time of appearance and numbers of fungus sporophores" (Wilkins and Harris, 1946). This work applied to seasonal phenology of mushroom production peaks as correlated with soil moisture in pinewood and beechwood habitats near Oxford University, England, and to fruiting-season peaks and rainfall in grassland habitat nearby (Wilkins and Patrick, 1940). Fogel (1976) reported an overall similar trend in the case of hypogeous fruiting bodies in a Douglas fir stand in western Oregon. These papers did not emphasize mushroom production as related to the total amount of summer rainfall. Montacchini and Caramiello (1968) did, however, report that summer rainfall affects the commercial production of mushrooms in Italy. My study experimentally confirms that increased total summer rainfall increased wild mushroom numbers and biomass.

The fact that only small- and medium-sized mushrooms responded to irrigation in my experiment was also predictable from the literature. Wilkins and Harris (1946), and Wilkins and Patrick (1940) observed that the seasonal peak of mushroom growth resulted mostly from a marked increase in numbers of only a few species of small-sized mushrooms. However, my results do not necessarily fit with the observations of Wilkins and Harris (1946) and Wilkins and Patrick (1940), since mushrooms in the present study were assigned to size-classes regardless of species and developmental stage. This may have had confounding effects, because some small and medium mushrooms were incompletely developed individuals of large species.

Fresh biomass of mushroom

Total fresh biomass of mushrooms was higher on irrigated grids than on controls, and this difference was statistically significant for 1996 (Table 8) but not for 1995, although all treatment grids had more biomass of mushrooms than their respective controls. The absence of statistical significance in 1995 was most likely due to high variances, a lower number of quadrats measured that year, and perhaps to lower contrasts in water input between treatments and controls. Also, biomass estimation in 1995 was less accurate than in 1996 (because biomass in 1995 was estimated using mid size-class diameters for small and medium mushrooms and minimum diameter for the larger ones). The 1996 data should be more representative since the methods were more rigorous.

To estimate fresh biomass I used an equation relating cap area to fresh biomass. Errors due to rounding of the cap diameter to the nearest 0.5 cm did not severely affect the contrast between treatment and control grids, as cap diameter was not different between grids (author, unpublished data). Therefore, the observed contrast in mushroom biomass between treatment and control grids depended on mushroom numbers rather than mushroom size. Some bias in biomass estimation might be due to the use of the 1995 correlation between cap area and fresh biomass for both experimental years, since this correlation can slightly vary from year to year (Krebs, unpublished data), perhaps because of mushroom water content. Fogel (1976) observed that "moisture content apparently varied with sporocarp age and soil moisture content". Further, Fogel (1976) found that moisture content varied between species. Hence, species composition of the sample could have had a small effect on the estimated relationship between cap area and fresh biomass.

Plants

The fact that the biomass of only one of the monitored species (*Arctostaphylos uva-ursi*) of the herbaceous strata clearly increased in response to the irrigation was surprising. Given that the vegetation in the area experiences summer water stress, I expected that many species would have reacted strongly to the treatment. White spruce trees were also expected to respond, since Basset (1964) demonstrated a clear correlation between growth in two species of conifers, *Pinus taeda* and *P. echinata*, and variations in soil moisture. I now consider potential causes for this apparent lack of response.

One of the most fundamental concerns about this experiment was whether irrigation levels were high enough to have any effect on the plant community. Irrigation enhanced watering levels to an average of 91% of the maximal rainfall experienced from 1973 to 1992 in the area. Therefore, if the yearly variations in rainfall affect the plant community significantly, this irrigation level should have affected plants to a greater extent than it did. Had the irrigation levels been higher than the maximal rainfall, the resulting effects would have been "unnatural" for the area, and hence could not explain natural variations in small mammal densities in the area. I can therefore conclude either that the sampling methods were improper for revealing plant responses, or else that most species were insensitive to the treatment. However, effects of long-term (multiple-year) trends in rainfall still cannot be overruled as having an effect on the plant community, but long-term monitoring would be required for verification.

A. uva-ursi occurred most consistently among subsamples, and represented the greatest average biomass per subsample (Appendix II). Therefore, the ability to detect statistical differences were greater for *A. uva-ursi* than for other species, since the statistical power (sample size) for that species was higher than for the other species. Hence, the apparent lack of response in some of the herbaceous strata species could be in part due to their poor representation in samples. Greater sampling effort would have led to a more accurate estimation of the different species' performance.

In white spruce, the lack of response in the lateral branch growth is not due to low sample size, as approximately 40 trees were sampled on each grid. However, one could argue

that the lateral growth itself is not a good indicator of total spruce response to irrigation. Granted that current photosynthesis can be limited by water availability (Boyer, 1976), growth of lateral branches, for example, might not depend on current photosynthesis as influenced by water deficit. In a discussion of maize production in response to reduced photosynthesis due to a water deficit, Boyer (1976) emphasized " [...] that plant reserves rather than current photosynthesis must have contributed dry weight to the grain". Hence, the measured LBG ratios in the present study might not follow solely from current photosynthetic rates, but might also depend on past reserves. Further, given that photosynthetic rate in white spruce is water-limited and that it reacted to the irrigation, it is possible that enhanced photosynthesis could have been invested in storage rather than growth. This storage response could result in either higher growth or increased cone production in later years. Similarly, this argument might hold for the ground-layer plants since they are perennials.

Another relevant issue is biomass partitioning within individual plants. The plants may have reacted to irrigation by increasing root production rather than increasing above-ground biomass. However, I consider this latter point unimportant in relation to vole densities, given that the trophic chain tested does not depend directly on root system production. Secondly, except for *A. uva-ursi* and *A. rubra*, reproductive output was not monitored, and therefore it is not known if the supplemental water influenced seed production, regardless of the response in above-ground vegetative tissues. This second point is probably of greater importance than the previous, since seed production could influence granivorous murid rodents.

Calculations of the water deficit also deserve consideration since some of the assumptions might be inadequate. First, Thornthwaite and Hare (1965) remarked that under certain conditions, vegetation type can have an important effect on evaporation calculations, but in general, water deficit calculated regardless of vegetation type remained valid (Thornthwaite and Hare, 1965). It is therefore likely that the vegetation at Kluane does experience a water deficit as calculated herein. Second, the depth of the root zone was assumed to be 150 mm, which might be erroneous. However, the early concepts and calculations of Thornthwaite (1948) assumed that "the available water under all but exceptionally deep root systems was constant with respect to plant and soil types". Therefore, the influence of the vegetation and soil type at Kluane in the calculation of the water deficit should be small, since spruce trees at Kluane are not deep-rooted. I therefore conclude that plants in Kluane undergo a summer water deficit.

The generalized lack of growth response to the treatment could alternatively be attributed to nitrogen limitation (Zasada *et al.*, 1977) rather than water availability. However, I expected that nitrogen availability itself would have increased in response to the treatment, since Binkley *et al.* (1994) demonstrated such a relationship between water and nitrogen availability. I therefore deduce that even if water was not the primary limiting resource, plants should have responded to irrigation anyway, owing to the anticipated increase in nitrogen availability in response to watering.

Finally, Grime (1977) considers plants of dry areas to be stress-tolerant, and hence, to have inherently slow growth rates. In his view, even when the stress in those species is relieved, they do not respond by growth. However, the response of *A. uva-ursi* in my study contradicts that expectation.

In summary, only *A. uva-ursi* responded to the treatment, while other plant species did not. The response of *A. uva-ursi* in the understory vegetation could be important, as it was the most common species in the herb strata (Appendix II) and its berry production could influence small mammals. Greater sampling effort could clarify the responses of other species, as could a more thorough analysis of the partitioning of growth within the plants themselves. Long-term monitoring would permit me to observe the effects of multiple-year variations in rainfall, and a potential storage response. Finally, a study of soil nitrogen availability would allow a better understanding of the factors limiting plant production in the area.

Invertebrates and shrews

Invertebrates showed no response to irrigation, apart from the centipedes and caterpillars which declined after treatment. This overall lack of response is surprising, since many parameters in insect life cycles are known to depend on humidity. Bursell (1964) points that "in most species which have been studied the rate of oviposition increases as the humidity is raised" . He further argues that development is usually retarded at low humidity (Buxton, 1932a). Further, some species are favored by rainfall through its influence on growth of food plants, as shown by Clark (1974). Given that in most plants no measure of performance

showed a reaction to the treatment, it is not surprising to see a lack of response in the invertebrates. However, I do not know if any species feed on *A. uva-ursi*, which reacted to the treatment in 1996. Otherwise, in the case where invertebrates would be predator-limited rather than food-limited (*sensu* Hairston *et al.*, 1960) the invertebrate densities might have been kept in check by predators, such as entomophagous invertebrates or shrews.

Shrews did not respond significantly to the irrigation treatment in 1995, although *Sorex monticolus* was consistently more numerous on the treatments than on the controls. On one hand, given the overall lack of response in the invertebrate community that year, the lack of significance in shrew reaction to the treatment was to be expected. The lack of measurable response could alternatively be due to predators consuming additional shrews, as explained by the "HSS" hypothesis (Hairston *et al.*, 1960). Again, further analysis of the 1996 data could help understand this lack of response.

It should be noted that pitfall trapping is only an index of invertebrate and shrew numbers, not a good estimation of density itself, as the effective area of trapping cannot be estimated. Hence, the results concerning those groups have to be interpreted with caution since sample sizes were relatively low.

Rodents

The aim of this experiment was to test for the existence of a bottom-up trophic chain on murid rodents, contingent on rainfall. I postulated that 1) murid densities in Kluane were food-limited, and 2) food sources were limiting because they themselves were limited by water

availability. A three-fold increase of *C. rutilus* (Boreal red-backed vole) on the irrigated grids relative to the controls was adopted as the criterion that would confirm the above two hypotheses, since artificial food-addition experiments show that food-limited populations undergo an increase of such a magnitude (Boutin, 1990). The response of *C. rutilus* to the irrigation treatment during the course of this study was uneven with respect to sites: the three-fold increase was not achieved on two of the three sites. On this basis, the above-mentioned hypotheses must either be rejected or revised.

Population densities of *C. rutilus* during the course of this experiment were abnormally low (especially at sites #1 and #3 which did not respond substantially to the treatment), potentially invalidating the results of this experiment with respect to rodents. On the control grids, the average densities in the autumn were 1 and 4 *C. rutilus* per grid for 1995 and 1996, respectively (Figures 11-13). In the same locality as my experiment, Gilbert and Krebs (1991) found such low densities in only 3 out of 13 years. Their overall average for 13 years was 17 animals per 2.3 ha (12 per 1.6 ha), which is 3 to 12 times higher than my average densities. I therefore suspect that the weak response to the irrigation at sites #1 and #3 might result from their atypically low baseline densities, especially since baseline densities at site #2 were higher and showed the predicted three-fold increase.

Apart from the unusually low vole densities, the top-down vs. bottom-up concepts could be invoked to explain the weak response at sites #1 and #3 of herbivorous murids to the treatment. The "HSS" hypothesis (Hairston *et al.*, 1960) proposes that herbivores are

predator-limited rather than food-limited (i.e. top-down population control). Fretwell (1987) argues that such can be the case only in trophic chains containing an uneven number of links. As the Kluane vertebrate community contains three links, plants, herbivores, predators, Fretwell's community model (1987) predicts that herbivores are predator-limited rather than food-limited. However, food addition experiments in Kluane have generated large population increases for mice and voles (Gilbert and Krebs, 1981), for hares (Krebs *et al.*, 1995), and for ground squirrels (Hubbs and Boonstra, 1997). Even if the community contained four trophic levels instead of three, Fretwell's (1987) model predicts that *C. rutilus* at the *second* trophic level would be food-limited rather than predator-limited, because their predators themselves would be limited by predators at the *fourth* level. Hence, even though predators limit hare and ground squirrels densities (Krebs *et al.*, 1995; Hubbs and Boonstra, 1997), food availability, *i.e.* bottom-up forces, influence herbivore densities at Kluane, contrary to Fretwell's (1987) and Hairston *et al.*'s (1960) predictions. I therefore conclude that the small response of *C. rutilus* on treatment grids #1 and #3 is unlikely to follow from the supremacy of top-down forces controlling their densities.

Perhaps the small response at sites #1 and #3 follows from the inability of the treatment to increase food sources adequately at those sites, and as put by Power (1992): "a green world might not be an edible one". In order to evaluate this argument, it is essential to know if the mushrooms and plants that reacted positively to the treatment were important food-sources for *C. rutilus*, and if they are, whether increased biomass would be enough to reduce food-limitation significantly.

The link between mushroom biomass, plant biomass, or berry numbers in *A. uva-ursi* and *C. rutilus* density is not supported by observation, as I did not verify if rodents fed on those items. Banfield (1974) specifies that *C. rutilus* feeds on fruit, leaves, buds, twigs and forbs, but mushrooms are not referred to. *A. uva-ursi* seems therefore to be the only species that could have had an effect on *C. rutilus*, since it was the only species which responded to the treatment and which is known to be part of this rodent's diet. Other plant species might be important to *C. rutilus*, but their response, if any, was not clear. Further, other plant parameters that were not monitored (such as spruce cones, for example) could have been more important than expected. A diet analysis in *C. rutilus* populations would be required to clarify the link between this rodent species and both *A. uva-ursi* and mushrooms, as well as other species of plants.

Second, the *quality* of those potential food sources was not monitored in this study, and according to White (1978, 1984), plant quality (*i.e.* assimilable nitrogen) is the limiting factor on herbivore densities. Hence, the small responses of *C. rutilus* (as well as herbivorous invertebrates discussed above) could be attributed to the incapacity of the treatment to affect plant quality. White (1978, 1984) further claims that plant quality increases when stressed. Therefore, my treatment consisting in reducing water stress in plants could have reduced plant quality: consequently, murid densities should have decreased under this hypothesis, which was not the case. On the other hand, White (1978, 1984) specifies that young tissues in plants are more nutritious than older ones. If irrigation increased the availability of young tissues (high quality food), perhaps rodent densities should increase. As White's model (1978, 1984) predicts both an increase and a decrease of plant quality in response to the irrigation

treatment, it cannot be used to make contrasting predictions in relation to my experiment. Analyses on plant assimilable nitrogen in response to irrigation and its effect on *C. rutilus* densities would be needed to clarify this point.

The above points demonstrate the need for further investigation to clarify the relationship between rainfall and vole numbers. Below, I elaborate on differences between site #2 and the others, first by pointing at the patterns of responses between the sites, then by emphasizing on control grid comparisons between sites.

Site #2 seemed to have responded in a much clearer way to the treatment than did the other sites. Not only was site #2 the only one where *C. rutilus* increased by the predicted 3-fold magnitude, but as well, only at that site were all three species of shrews in greater numbers on the treatment grid than on the control. Additionally, more species of the understory vegetation had a greater biomass on T/2 than C/2 as compared to the other sites. Moreover, invertebrate taxa responded more consistently on site #2, with 7 out of 9 groups being lower on T/2 than on C/2, while only about half of the groups were either higher or lower on the treatment grids compared to the controls at the other sites. It therefore seems that only at site #2 did most trophic levels respond to the irrigation in a consistent manner.

This striking difference between site #2 and the two other sites could be due to one of the three following possibilities: 1) T/2 is inherently more productive than C/2; 2) random sampling biases at T/2 converged; and 3) site #2 was unique in its reaction to the treatment.

Control grid comparisons between-sites indicate that baseline parameter values found at C/2 were substantially different from those at the two other control grids, which suggests that possibility #3 is the most likely explanation.

Vole density on C/2 was the highest of all control grids, and many other groups had higher baseline values on C/2 than on the other control grids. C/2 had both greater numbers and biomass of mushrooms for all size-classes (1995 and 1996), had the highest *A. uva-ursi* berry numbers and biomass per permanent quadrat (1996), had the highest number and biomass of both ground beetles and total invertebrates (fall 1995), and had the greatest number of grasshoppers. Conversely, C/2 had a lower biomass of *A. uva-ursi* and total understory vegetation biomass, and had fewer shrews.

Considering the above contrasts between both T/2 and C/2 and between C/2 and the other controls, I therefore believe that the striking responses to the irrigation at T/2 follow from its baseline values, and not from converging sampling biases nor from T/2 being inherently more productive than C/2. I suspect that the response of *C. rutilus* to the irrigation treatment might be strongly influenced by site characteristics. First, perhaps higher baseline values in many trophic parameters at site #2 allowed higher baseline densities in *C. rutilus* at that site, which in turn allowed their densities to increase more (as compared to the other sites) in response to enhanced trophic production due to the irrigation. Second, it is also possible that the greater increase in vole numbers at T/2 (as compared to the other treatment grids) follows from the generally larger and more consistent trophic parameter increases in response to the irrigation.

Conclusion

This study offers only partial support for the influence of rainfall on vole densities, since the amplitude of the responses in many parameters was site-specific and often weaker than predicted. However, both vole numbers and some of their potential food-sources were generally higher on the irrigated grids than on the controls, and unlike sites #1 and #3, site #2 showed substantial responses in most parameters, including vole densities. Therefore, I believe that it would be more sound to revise the hypotheses (namely that murid densities in Kluane are limited by the availability of food which in turn is limited by water availability) rather than rejecting them. Baseline vole densities, as well as baseline trophic production (which might influence the amplitude of increase in trophic parameters), might modulate vole response to rainfall.

In order to better understand those relationships, studies should be done while *C. rutilus* densities are more typical than during the course of this study. To clarify the apparent lack of response in many plant species, further studies should include both long-term monitoring of plant performance to determine storage responses, and analysis of nitrogen availability in the soil. Diet analyses in *C. rutilus* should be done to determine the relationship between this species and both the plants and mushrooms that responded to the treatment. Moreover, plant quality response to irrigation should be investigated, as a lack of response in quality could have affected the response of rodents.

Literature cited

Banfield, A.W.F. 1974. The mammals of Canada. University of Toronto Press, 438 p.

Basset, J.R. 1964. Tree growth as affected by soil moisture availability. Soil Sci. Soc. Am. Proc. **28**: 436-438.

Beatley, J.C. 1969. Dependence of desert rodents on winter annuals and precipitation. Ecology **50**(4): 721-724.

Beatley, J.C. 1976. Rainfall and fluctuating plant populations in relation to distributions and numbers of desert rodents in southern Nevada. Oecologia **24**: 21-42.

Bernard, E. 1945. Le climat écologique de la cuvette centrale congolaise. Publications de l'Institut National pour l'étude agronomique du Congo Belge, Bruxelles. *In*: Thornthwaite, C.W. and F.K. Hare. 1965. The loss of water to the air. Meteorological monographs **6**(28):163-180.

Binkley, D., R. Stottlemyer, F. Suarez and J. Cortina. 1994. Soil nitrogen availability in some arctic ecosystems in northwest Alaska: Responses to temperature and moisture. Ecoscience **1**(1): 64-70.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. Can. J. Zool. **68**: 203-220.

Boyer, J.S. 1976. Water deficits and photosynthesis. *in*: Kozlowski, T.T. 1976. Water deficits and plant growth, Vol. 4. Academic Press, N.-Y. pp. 153-190.

Bursell, E. 1964. Environmental aspects: Humidity. pp.323-361 *in*: Rockstein, M. 1964. Physiology of insecta, Volume 1. Academic Press, N.Y., 640 p.

Buxton, P. A. 1932a. Biol. Rev. Cambridge Phil. Soc. **7**: 275. *In*: Bursell, E. 1964. Environmental aspects: Humidity. pp.323-361 *in*: Rockstein, M. 1964. Physiology of insecta, Volume 1. Academic Press, N.Y., 640 p.

Clark, D.P. 1974. The influence of rainfall on the densities of adult *Chortoicetes terminifera* (Walker) in Central Western New South Wales, 1965-73. Aust. J. Zool. **22**: 365-86.

Douglas, G.W. 1974. Montane zone vegetation of the Alsek River region, southwestern Yukon. Can. J. Bot. **52**(6): 2505-2532.

Dunigan, P.F.X. Jr., W. Lei, and W.H. Rickard. 1980. Pocket mouse population response to winter precipitation and drought. Northwest Science **54**(4): 289-295.

Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas Fir stand. Can. J. Bot. **54**: 1152-1162.

Fretwell, S.D. 1987. Food chain dynamics: the central theory of ecology? Oikos **50**: 291-301.

Frontier, S. and D. Pichod-Viale. 1990. Écosystèmes: structure, fonctionnement, évolution. Éd. Masson, Paris, 392 p.

Gilbert, B.S. and C.J. Krebs. 1981. Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the Southwestern Yukon. Oecologia **51**: 326-331.

Gilbert, B.S. and C.J. Krebs. 1991. Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon 1973-1989. Holarctic Ecology **14**: 250-259.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat.**111**: 1169-1194.

Hairston, N.G., Smith, F.E. and L.B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**: 421-425.

Hubbs, A.H. and R. Boonstra. 1997. Population limitation in Arctic ground squirrels: effects of food and predation. J. An. Ecol. **66**: 527-541.

Krebs, C.J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs **36**: 239-273.

Krebs, C.J. 1995. Kluane Project handbook of field procedures 1995. Unpublished.

Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K. and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269**: 1112-1115.

Krebs, C.J. and I. Wingate. 1985. Population fluctuations in the small mammals of the Kluane region, Yukon Territory. Canadian Field-Naturalist **99**(1): 51-61.

Krebs, C.J. and I. Wingate. 1976. Small mammal communities of the Kluane region, Yukon Territory. Canadian Field-Naturalist **90**(4): 379-389.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology **59**(3): 465-472.

Montacchini, F. and R. Caramiello. 1968. Ecologia del *Tuber magnatum* Pico in Piemonte. Allionia **14**: 1-29. *In*: Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas Fir stand. Can. J. Bot. **54**: 1152-1162.

Power, M.E. 1992. Top-down and bottom-up forces in food webs: do plants have supremacy? Ecology **73**(3): 733-746.

Rowe, J.S. 1972. Forest regions of Canada. Department of the Environment, Canadian Forestry Service. Publication No. 1300. 171 p.

Thornthwaite, C.W. 1962. Average climatic water-balance of the continents part VI (North America). Publications in Climatology **17**(2): 234-414.

Thornthwaite, C.W. and F.K. Hare. 1965. The loss of water to the air. Meteorological monographs **6**(28):163-180.

Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology **63**(4): 992-1003.

van Zyll de Jong, C.G. 1983. Handbook of Canadian mammals, V. 1: Marsupials and Insectivores. National Museums of Canada, 210 p.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia **33**: 71-86.

White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia **63**: 90-105.

Wilkins, W.H. and G.C.M. Harris. 1946. The ecology of larger fungi: V. An investigation into the influence of rainfall and temperature on the seasonal production of fungi in a beechwood and pinewood. J. Appl. Biol. **33**: 179-188.

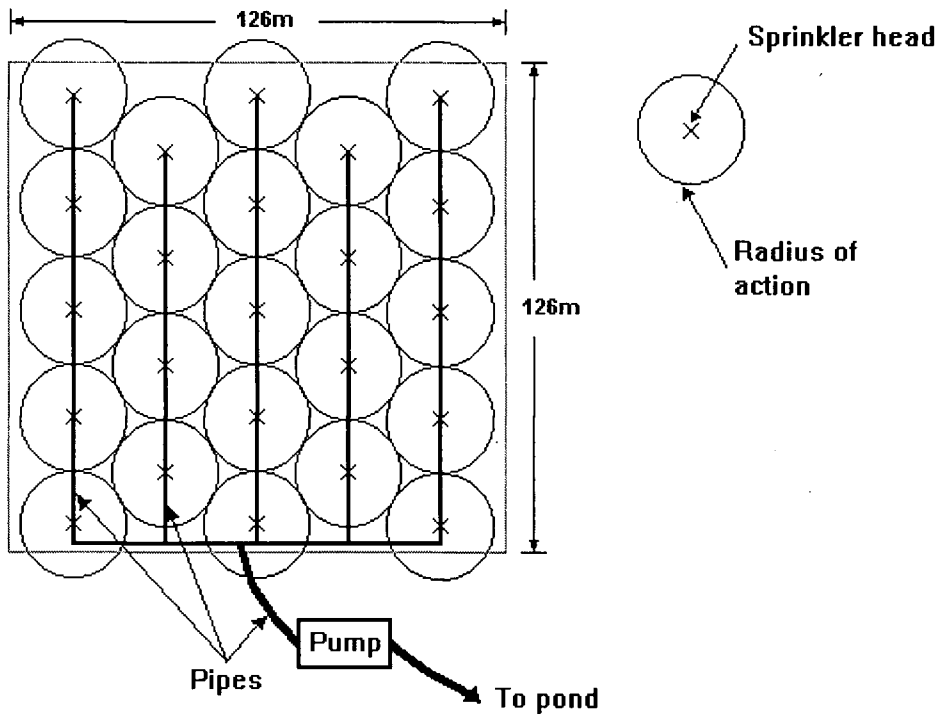
Wilkins, W.H. and S.H.M. Patrick. 1940. The ecology of larger fungi: IV. The seasonal frequency of grassland fungi with special reference to the influence of environmental factors. Ann. Appl. Biol. **27**: 17. *In*: Wilkins, W.H. and G.C.M. Harris. 1946. The ecology of larger fungi: V. An investigation into the influence of rainfall and temperature on the seasonal production of fungi in a beechwood and pinewood. J. Appl. Biol. **33**: 179-188.

Zasada, J.C., K. Van Cleve, R.A. Werner, J.A. McQueen and E. Nyland. 1977. Forest research and management at high latitudes *in*: North-American forest lands at latitudes north of 60 degrees. Proceedings of a symposium held at the University of Alaska, Fairbanks September 19, 20, 21 and 22, 1977. pp.137-195.

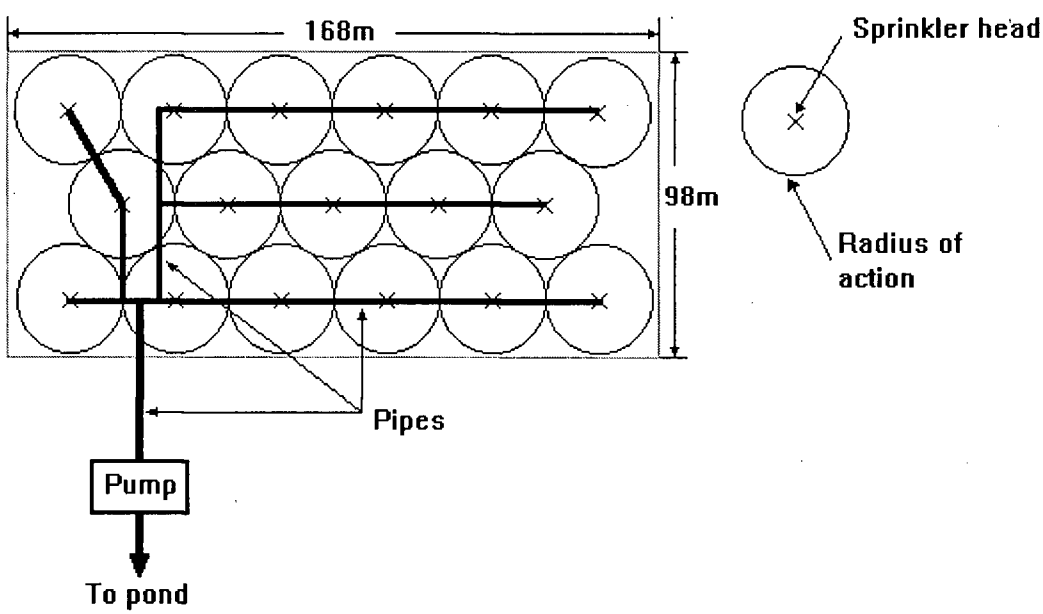
Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall Inc. Englewood Cliffs, N-J, 718 p.

Appendix I: Irrigation system design: a) grids T/1 and T/2; b) grid T/3.

a)



b)



Appendix II: Herbaceous strata plant biomasses (g dry weight) per group for all grids. A) Spring and fall 1995, averages calculated using all samples. Treatment grids in bold.

	Group	C/1	**T/1**	C/2	**T/2**	C/3	**T/3**
	N	34	**34**	32	**33**	30	**30**
	Arctostaphylos uva-ursi	3.93	**3.47**	2.14	**4.55**	2.55	**2.52**
	Linnaea borealis	0.26	**0.00**	0.38	**0.35**	0.74	**0.17**
Spring	Others	1.25	**1.01**	0.86	**0.57**	1.44	**1.45**
	All herbaceous	1.51	**1.01**	1.24	**0.92**	2.18	**1.65**
	Total	5.44	**4.48**	3.39	**5.47**	4.74	**4.14**
	N	33	**33**	34	**33**	24	**30**
	Arctostaphylos uva-ursi	6.22	**6.13**	1.16	**5.57**	3.04	**2.33**
	Linnaea borealis	0.08	**0.00**	0.10	**0.58**	0.63	**0.37**
Fall	Others	1.15	**1.10**	1.25	**0.92**	1.19	**1.03**
	All herbaceous	1.23	**1.10**	1.35	**1.49**	1.82	**1.41**
	Total	7.46	**7.23**	2.51	**7.06**	4.86	**3.73**

Appendix II: Average herbaceous strata plant biomasses (g dry weight) per group for all grids. B) Spring and fall 1995, averages calculated using only samples where investigated taxa were present. Treatment grids in bold.

		C/1		**T/1**		C/2		**T/2**		C/3		**T/3**	
	Group	N	Mass(g)	**N**	**Mass(g)**	N	Mass(g)	**N**	**Mass(g)**	N	Mass(g)	**N**	**Mass(g)**
	Arctostaphylos uva-ursi	23	6.17	**27**	**4.37**	13	5.28	**23**	**6.53**	23	3.33	**21**	**3.99**
	Linnaea borealis	5	1.79	**0**	**0.00**	9	1.37	**13**	**0.89**	17	1.31	**7**	**0.91**
Spring	Others	29	1.47	**32**	**1.08**	32	0.89	**30**	**0.63**	28	1.54	**30**	**1.66**
	All herbaceous	30	1.72	**32**	**1.08**	31	1.28	**30**	**1.02**	28	2.34	**30**	**1.88**
	Total	30	6.44	**32**	**4.76**	31	3.50	**30**	**6.02**	28	5.07	**30**	**4.67**
	Arctostaphylos uva-ursi	27	7.61	**30**	**6.74**	12	3.28	**20**	**9.18**	20	3.64	**19**	**3.68**
	Linnaea borealis	1	2.70	**0**	**0.00**	7	0.47	**12**	**1.59**	12	1.27	**10**	**1.12**
Fall	Others	28	1.36	**29**	**1.26**	30	1.42	**30**	**1.01**	24	1.19	**28**	**1.11**
	All herbaceous	28	1.46	**29**	**1.26**	31	1.48	**32**	**1.54**	24	1.82	**28**	**1.51**
	Total	32	7.69	**33**	**7.23**	32	2.67	**32**	**7.28**	24	4.86	**28**	**4.00**

Appendix II: Average herbaceous strata plant biomasses (g dry weight) per group. C) Spring and fall 1995 Mann-Whitney U and p values, for both averages using all samples and averages using only samples where investigated taxa were present.

		Spr ing		Fa ll	
	Group	U	p	U	p
	Arctostaphylos uva-ursi	2.000	0.28	4.000	0.83
	Linnaea borealis	8.000	0.13	5.000	0.83
All samples	others	5.000	0.83	9.000	**0.05**
	All herbaceous plants	7.000	0.28	5.000	0.83
	All plants	5.000	0.83	4.000	0.83
	Arctostaphylos uva-ursi	4.000	0.83	2.000	0.28
Non-zero	*Linnaea borealis*	9.000	**0.05**	6.000	0.51
samples	others	5.000	0.83	8.000	0.13
	All herbaceous plants	7.000	0.28	5.000	0.83
	All plants	5.000	0.83	4.000	0.83

Appendix II: Herbaceous strata plant biomasses (g dry weight) per group for all grids. D) Spring 1996, averages calculated using all samples. Treatment grids in bold.

Group	C/1 N=23	**T/1 N=23**	C/2 N=23	**T/2 N=23**	C/3 N=18	**T/3 N=17**
Arctostaphylos uva-ursi	3.40	**10.07**	5.10	**7.63**	8.50	**3.42**
A. uva-ursi fruit number	0.30	**1.83**	2.13	**2.26**	0.72	**0.94**
A. uva-ursi fruit mass	0.03	**0.13**	0.14	**0.18**	0.05	**0.06**
A. uva-ursi total	3.42	**10.20**	5.24	**7.82**	8.54	**3.48**
A. rubra	0	**0**	0	**0**	0.36	**0.01**
A. rubra fruit number	0	**0**	0	**0**	0	**0**
A. rubra fruit mass	0	**0**	0	**0**	0	**0**
A. rubra total	0	**0**	0	**0**	0.36	**0.01**
Grass	0.48	**0.45**	0.50	**0.68**	0.24	**0.84**
Equisetum spp.	0	**0**	0.17	**0.07**	0.77	**0.20**
Epilobium latifolia	0	**0**	0.03	**0**	0	**0.01**
Achillea millefolium	0.01	**0.01**	0.02	**0.02**	0.04	**0.04**
Linnaea borealis	0	**0**	0.26	**0.49**	0.88	**0.49**
Others	0.04	**0.11**	0.11	**0.06**	0.23	**0.30**
All herbaceous plants	0.53	**0.58**	1.09	**1.33**	2.17	**1.89**
All plants	4.26	**12.61**	8.46	**11.41**	11.80	**6.27**

Appendix II: Average herbaceous strata plant biomasses (g dry weight) per group for all grids. E) Spring 1996, averages calculated using only samples where investigated taxa where present. Treatment grids in bold.

	C/1		**T/1**		C/2		**T/2**		C/3		**T/3**	
Group	N	Mass(g)	N	**Mass(g)**	N	Mass(g)	N	**Mass(g)**	N	Mass(g)	N	**Mass(g)**
Arctostaphylos uva-ursi	19	4.11	21	**11.03**	13	9.03	17	**10.33**	14	10.93	14	**4.16**
A. uva-ursi fruit number	2	3.50	11	**3.82**	7	7.00	10	**5.20**	6	0.50	5	**3.00**
A. uva-ursi fruit mass	2	0.30	11	**0.28**	7	0.46	10	**0.43**	6	0.02	5	**0.19**
A. uva-ursi total	19	4.14	21	**11.17**	13	9.28	17	**10.58**	14	10.98	14	**4.23**
A. rubra	0	0	0	**0**	1	0.05	0	**0**	11	0.59	1	**0.11**
A. rubra fruit number	0	0	0	**0**	0	0	0	**0**	0	0	0	**0**
A. rubra fruit mass	0	0	0	**0**	0	0	0	**0**	0	0	0	**0**
A. rubra total	0	0	0	**0**	1	0.05	0	**0**	11	0.59	1	**0.11**
Grass	21	0.52	20	**0.52**	23	0.50	20	**0.79**	16	0.27	15	**0.90**
Equisetum spp.	1	0.06	0	**0**	14	0.28	10	**0.17**	17	0.82	15	**0.23**
Epilobium latifolia	0	0	3	**0.01**	7	0.09	2	**0.05**	4	0.02	4	**0.05**
Achillea millefolium	6	0.04	7	**0.03**	10	0.05	8	**0.05**	11	0.06	11	**0.07**
Linnaea borealis	0	0	0	**0**	6	1.00	9	**1.24**	14	1.14	5	**1.68**
Others	14	0.06	14	**0.19**	15	0.17	16	**0.09**	18	0.23	15	**0.34**
All herbaceous plants	23	0.53	23	**0.58**	23	1.09	23	**1.33**	18	2.17	16	**1.95**
All plants	23	4.26	23	**12.61**	23	8.46	23	**11.41**	18	11.80	17	**6.27**

Appendix II: Herbaceous strata plant biomasses (g dry weight) per group for all grids. F) Fall 1996, averages calculated using all samples. Treatment grids in bold.

Group	C/1 N=23	**T/1 N=23**	C/2 N=23	**T/2 N=24**	C/3 N=17	**T/3 N=17**
Arctostaphylos uva-ursi	4.30	**8.24**	3.25	**4.85**	4.19	**7.62**
A. uva-ursi fruit number	0.74	**1.52**	0.70	**2.67**	1.24	**1.57**
A. uva-ursi fruit mass	0.04	**0.08**	0.05	**0.11**	0.07	**0.18**
A. uva-ursi total	4.34	**8.32**	3.30	**4.96**	4.26	**7.55**
A. rubra	0	**0**	0.05	**0.07**	1.96	**0.59**
A. rubra fruit number	0	**0**	0.04	**0.21**	0.88	**0.06**
A. rubra fruit mass	0	**0**	0	**0.01**	0.03	**0**
A. rubra total	0	**0**	0.05	**0.07**	1.98	**0.59**
Grass	1.38	**1.26**	1.01	**1.51**	0.38	**0.65**
Equisetum spp.	0	**0**	0.15	**0.05**	0.69	**0.24**
Epilobium latifolia	0.57	**0.56**	0.12	**0.06**	0.05	**0.21**
Achillea millefolium	0.04	**0.01**	0.01	**0.02**	0.06	**0.08**
Linnaea borealis	0.14	**0**	0.53	**0.41**	1.02	**0.44**
Others	0.18	**0.20**	0.36	**0.19**	0.58	**0.38**
All herbaceous plants	2.31	**2.04**	2.18	**2.23**	2.78	**1.86**
All plants	6.65	**10.36**	5.53	**7.27**	9.02	**10.02**

Appendix II: Average herbaceous strata plant biomasses (g dry weight) per group for all grids. G) Fall 1996, averages calculated using only samples where investigated taxa where present. Treatment grids in bold.

	C/1		**T/1**		C/2		**T/2**		C/3		**T/3**	
Group	N	Mass(g)	N	**Mass(g)**	N	Mass(g)	N	**Mass(g)**	N	Mass(g)	N	**Mass(g)**
Arctostaphylos uva-ursi	20	4.94	21	**9.02**	11	6.80	17	**6.85**	11	6.48	11	**11.53**
A. uva-ursi fruit number	6	2.83	8	**4.38**	4	4.00	10	**6.40**	5	4.20	6	**3.83**
A. uva-ursi fruit mass	6	0.17	8	**0.24**	4	0.27	10	**0.27**	5	0.22	6	**0.16**
A. uva-ursi total	20	5.00	21	**9.11**	11	6.90	17	**7.01**	11	6.58	11	**11.61**
A. rubra	0	0	0	**0**	1	0.04	2	**0.81**	12	2.77	4	**2.37**
A. rubra fruit number	0	0	0	**0**	1	1.00	1	**5.00**	3	5.00	1	**1.00**
A. rubra fruit mass	0	0	0	**0**	1	0.04	1	**0.13**	3	0.15	1	**0.20**
A. rubra total	0	0	0	**0**	1	1.16	2	**0.88**	12	2.81	4	**2.38**
Grass	22	1.44	21	**1.38**	23	1.01	23	**1.57**	16	0.41	15	**0.77**
Equisetum spp.	0	0	0	**0**	16	0.22	12	**0.09**	17	0.69	15	**0.24**
Epilobium latifolia	11	1.19	10	**1.29**	4	0.71	5	**0.28**	4	0.20	6	**0.32**
Achillea millefolium	9	0.11	3	**0.05**	7	0.03	12	**0.04**	7	0.14	11	**0.16**
Linnaea borealis	2	1.56	1	**0.11**	8	1.51	9	**1.23**	13	1.33	8	**1.09**
Others	18	0.23	13	**0.35**	16	0.51	20	**0.24**	17	0.58	17	**0.43**
All herbaceous plants	22	2.41	22	**2.13**	23	2.18	23	**2.33**	17	2.78	17	**2.04**
All plants	23	6.65	23	**10.36**	23	5.53	24	**7.27**	17	9.02	17	**10.02**

Appendix II: Average herbaceous strata plant biomasses (g dry weight) per group. H) Spring and fall 1996 Mann-Whitney U and p values, for both averages using all samples and averages using only samples where investigated taxa were present.

		Spr ing		Fa ll	
	Group	U	p	U	p
All samples	*Arctostaphylos uva-ursi*	3.000	0.51	0.000	**0.05**
	A. uva-ursi fruit number	2.000	0.28	0.000	**0.05**
	A. uva-ursi fruit mass	2.000	0.28	0.000	**0.05**
	A. uva-ursi total	3.000	0.51	0.000	**0.05**
	A. rubra	5.000	0.80	4.500	1.00
	A. rubra fruit number	4.500	1.00	4.500	1.00
	A. rubra fruit mass	4.500	1.00	5.000	0.80
	A. rubra total	5.000	0.80	4.500	1.00
	Grass	2.000	0.28	3.000	0.51
	Equisetum spp.	5.500	0.66	5.500	0.66
	Epilobium latifolia	5.000	0.80	4.000	0.83
	Achillea millefolium	4.500	1.00	4.500	1.00
	Linnaea borealis	4.500	1.00	7.000	0.28
	Others	3.500	0.66	5.000	0.83
	All herbaceous plants	4.000	0.83	8.000	0.13
	All plants	3.000	0.51	1.000	0.13
Non-zero samples	*Arctostaphylos uva-ursi*	3.000	0.51	0.000	**0.50**
	A. uva-ursi fruit number	4.000	0.83	2.000	0.28
	A. uva-ursi fruit mass	5.000	0.83	4.500	1.00
	A. uva-ursi total	3.000	0.51	0.000	**0.05**
	A. rubra	6.000	0.48	4.500	1.00
	A. rubra fruit number	4.500	1.00	4.500	1.00
	A. rubra fruit mass	4.500	1.00	3.500	0.66
	A. rubra total	4.500	1.00	5.500	0.66
	Grass	0.500	0.08	3.000	0.51
	Equisetum spp.	7.000	0.28	5.500	0.66
	Epilobium latifolia	4.000	0.83	4.000	0.83
	Achillea millefolium	4.500	1.00	4.000	0.83
	Linnaea borealis	2.500	0.38	9.000	**0.05**
	Others	3.000	0.51	6.000	0.51
	All herbaceous plants	4.000	0.83	8.000	0.13
	All plants	3.000	0.51	1.000	0.13

Appendix III: Spring and fall 1995 average numbers of selected ground-dwelling invertebrates caught per trap per day on each grid (a), their average biomass (b), and Mann-Whitney U and p values (c).

a)

	Grid	N	Days	Spiders	Carabidae	Cicadellidae*	Cicadellidae**	Lepidoptera***	Grasshoppers	Silphidae	Centipedes	Snails	Total
	C/1	25	23	1.2609	0.1687	0.0261	1.8087	0.0783	0.0052	0	0.0139	0.0017	3.9304
	T/1	25	23	1.0017	0.2243	0.0243	0.7687	0.0626	0.0087	0.0087	0.0087	0	2.3461
Spring	C/2	15	32	0.7979	0.0563	0.0083	0.5521	0.0333	0.0313	0.0021	0.0083	0.0083	1.5458
	T/2	15	32	0.8292	0.0979	0.0021	0.4479	0.0167	0.0083	0	0	0.0042	1.4375
	C/3	23	10	0.4217	0.0826	0	0.0217	0.0217	0.0043	0	0.0174	0.0261	0.6391
	T/3	21	10	0.5238	0.0762	0	0.1095	0.0095	0	0.0095	0.0143	0.0190	0.7857
	C/1	19	26	0.2490	0.0425	1.2976	0.3502	0.0668	0.0911	0.0182	0.0202	0.0263	2.2490
	T/1	25	26	0.2723	0.0646	1.9477	0.4185	0.0169	0.0815	0.0615	0.0015	0.0015	2.9354
Fall	C/2	19	19	0.4681	0.0665	1.9086	0.8366	0.0831	0.1274	0.0139	0.0083	0.0028	3.5319
	T/2	24	19	0.4342	0.0746	0.2303	0.3158	0.0285	0.0987	0.0175	0.0044	0.0022	1.2105
	C/3	20	26	0.4962	0.0288	0.0308	0.0962	0.0442	0.0577	0.0308	0.0115	0.0481	0.8712
	T/3	20	26	0.2942	0.0346	0.1808	0.2154	0.0481	0.0288	0.0346	0.0019	0.0269	0.8788

*: Unidentified large species

**: Unidentified other species

***: Larvae of both lepidoptera and hymenoptera

b)

	Grid	N	Days	Spiders	Carabidae	Cicadellidae*	Cicadellidae**	Lepidoptera***	Total
	C/1	25	23	0.0099	0.0040	0.0001	0.0005	0.0009	0.0179
	T/1	25	23	0.0076	0.0099	0.0001	0.0002	0.0011	0.0202
Spring	C/2	15	32	0.0043	0.0017	0	0.0001	0.0001	0.0065
	T/2	15	32	0.0039	0.0065	0	0.0001	0.0001	0.0107
	C/3	23	10	0.0029	0.0038	0	0	0.0002	0.0072
	T/3	21	10	0.0028	0.0041	0	0.0001	0	0.0070
	C/1	19	26	0.0013	0.0020	0.0023	0.0002	0.0018	0.0076
	T/1	25	26	0.0016	0.0030	0.0034	0.0002	0.0004	0.0086
Fall	C/2	19	19	0.0028	0.0024	0.0036	0.0004	0.0012	0.0101
	T/2	24	19	0.0025	0.0052	0.0004	0.0001	0.0006	0.0088
	C/3	20	26	0.0032	0.0007	0.0001	0	0.0013	0.0057
	T/3	1	26	0.0018	0.0005	0.0003	0.0001	0.0010	0.0033

*: Unidentified large species

**: Unidentified other species

***: Larvae of both lepidoptera and hymenoptera

Appendix III (Continued)

c)

	Group	Spr ing U	Spr ing p	Fa ll U	Fa ll p
Numbers	Spiders	4.000	0.83	6.000	0.51
	Carabidae	3.000	0.51	3.000	0.51
	Cicadellidae*	5.500	0.66	4.000	0.83
	Cicadellidae**	5.000	0.83	5.000	0.83
	Lepidoptera***	7.000	0.28	8.000	0.13
	Grasshoppers	5.000	0.83	6.000	0.51
	Silphidae	2.000	0.25	2.000	0.28
	Centipedes	6.000	0.51	9.000	**0.05**
	Snails	6.000	0.51	7.000	0.28
	Total	5.000	0.83	5.000	0.83
Dry Biomass (g)	Spiders	6.000	0.51	6.000	0.51
	Carabidae	0.000	**0.05**	3.000	0.51
	Cicadellidae*	4.500	1.00	5.000	0.83
	Cicadellidae**	4.000	0.82	5.500	0.83
	Lepidoptera***	5.500	0.66	9.000	**0.05**
	Total	3.000	0.51	5.000	0.83

*: Unidentified large species
**: Unidentified other species
***: Larvae of both lepidoptera and hymenoptera

Appendix IV: Mann-Whitney U and p values for average body weight (g) differences between treatment and control grids for *Clethrionomys rutilus* at each site for three trapping sessions when applicable.

Site	Fall 1995	Spring 1996	Fall 1996
1	n/a n/a	U = 0.000 p = 0.08	U = 4.000 p = 0.56
2	n/a n/a	U = 6.000 p = 0.77	U = 3.500 p = 0.23
3	n/a n/a	n/a n/a	n/a n/a