

Trophic effects of rainfall on *Clethrionomys rutilus* voles: an experimental test in a xeric boreal forest in the Yukon Territory

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Abstract: The Kluane forest is unusual in that it is less productive than other boreal forests because it lies in a rain-shadow zone. Densities of the boreal red-backed vole *Clethrionomys rutilus* are known to be food-limited in the Kluane region, and its food sources (mostly plants) could be rainfall-limited. We therefore tested the hypothesis that rainfall indirectly controlled vole densities in the Kluane region. Our predictions were that (i) food for voles would increase with additional rainfall and (ii) food-limited voles would in turn increase in numbers. Three sites in the Kluane forest were irrigated during the growing season for 5 years, and these were compared with three paired control sites without irrigation. Irrigation increased rainfall 91% above normal, on average. Neither understory plants, trees, invertebrates, nor the vole population reacted to irrigation. Only mushroom biomass increased. Hence, the above hypothesis must be rejected. The vegetation is not directly water-limited at these sites, and nitrogen limitation probably prevailed. However, mushroom biomass increased with irrigation and in turn should have increased nitrogen mineralization. It is therefore unclear why plant production and vole numbers did not increase with mushroom biomass on the irrigated sites.

Résumé : La productivité primaire de la forêt de Kluane est inférieure à celle des autres forêts boréales en raison du microclimat xérique qui y règne. Les densités du campagnol *Clethrionomys rutilus* sont limitées par l'abondance de nourriture dans la région de Kluane et ces sources de nourriture (principalement des plantes) pourraient y être limitées par la sécheresse. Nous avons donc testé l'hypothèse selon laquelle l'abondance des pluies contrôle de manière indirecte les densités de campagnols dans la forêt de Kluane. Nos prédictions étaient que (i) l'ajout expérimental de pluie augmenterait la production de nourriture des campagnols et (ii) la densité de campagnols en serait plus élevée. Durant 5 étés, nous avons irrigué trois sites expérimentaux dans la forêt de Kluane puis les avons comparés à trois sites témoins. Les sites irrigués ont reçu en moyenne 91 % plus de pluie que les sites témoins. La biomasse de champignons a fortement augmenté suite à l'irrigation, mais aucune réponse ne fut détectée du côté des plantes herbacées, des arbres, des invertébrés ou des campagnols. Notre hypothèse doit donc être rejetée. La faible croissance végétale dans la région de Kluane n'est donc pas directement liée aux conditions xériques; c'est plutôt le manque d'azote dans le sol qui semble en être responsable. Cependant, l'accroissement de la biomasse de champignons aurait dû logiquement s'accompagner d'une plus grande minéralisation de l'azote, ce qui aurait eu pour effet de stimuler les plantes. Il n'est donc pas clair pourquoi la production des plantes et le nombre de campagnols n'ont pas augmenté avec la hausse de la biomasse des champignons sur les sites irrigués.

Introduction

In the Kluane boreal forest, Yukon Territory, Canada, populations of boreal red-backed voles (*Clethrionomys rutilus*) fluctuate in an irregular fashion. Vole densities are usually low, but unpredictable outbreaks occur (Krebs and Wingate 1985; Gilbert and Krebs 1991). Although the causes for these outbreaks are not clear, year-to-year variations in food abundance could be a factor determining vole densities because both Gilbert and Krebs (1981) and Schweiger and Boutin (1995) obtained rapid population increases in food-addition experiments. Plants, the food source for voles (Banfield 1974), could in turn be rainfall-limited because the

region undergoes a water deficit during summer (Fig. 1) because of the rain shadow of the St. Elias Mountains (Rowe 1972). Water deficits reduce photosynthetic activity (Boyer 1976; Hellkvist et al. 1980; Teskey et al. 1994) as well as plant growth (e.g., Basset 1964). Above-average rainfall in the Kluane region could reduce the summer water deficit, which would in turn enhance primary production and reduce food limitation in voles, ultimately leading to a population outbreak.

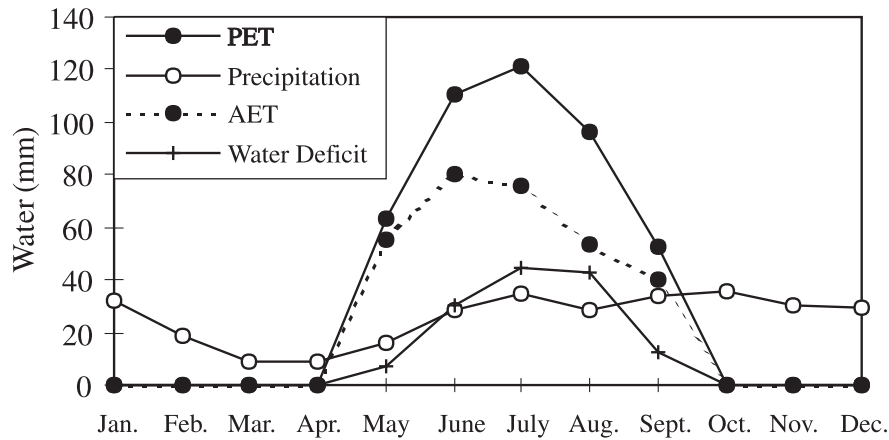
Trophic resources other than plants might further fuel this bottom-up trophic linkage mediated by rainfall. Rates of soil microbial activity such as litter decomposition (Meentemeyer 1978) and soil nitrogen mineralization (Binkley et al. 1994) increase as soil moisture increases. Above-average rainfall should increase the decomposition rate and nitrogen availability, further enhancing plant production, which is also nitrogen-limited in the Kluane region (Turkington et al. 1998). At the same time, production of food sources other than plants might respond to increased rainfall and therefore reduce food limitation in voles. For instance, mushroom production correlates with rainfall (Wilkins and Harris 1946; Montacchini and Caramiello 1968; Fogel 1976), and some

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Fig. 1. Average monthly water balance for Haines Junction, Yukon Territory, showing a water deficit for each of the summer months. Climate normals 1944–1985 are from Canadian Meteorological Centre (2001). Calculation methods are from Thornthwaite and Mather (1957). Soil water retention is assumed to be 300 mm. PET, potential evapotranspiration; AET, actual evapotranspiration.



insects proliferate as a result of bottom-up trophic flows triggered by increased rainfall (Clark 1974). Further, in many insects, survival rate, speed of development, and number of eggs laid per female also correlate with relative humidity (Bursell 1964).

We tested the hypothesis that rainfall indirectly controls vole densities in the Kluane boreal forest through changes in plant production. Our predictions were therefore that (i) the biomass of plants and other food sources for voles would increase as precipitation increased, and (ii) food-limited voles would in turn proliferate in response to this increase in food production. We experimentally tested these two predictions by irrigating three sites in the boreal forest from 1995 to 1999, and concurrently comparing numbers of voles and availability of their potential food sources such as mushrooms, understory vegetation, white spruce (*Picea glauca*) trees, and forest-floor invertebrates between irrigated and nearby non-irrigated sites.

Materials and methods

Study area and experimental sites

The study area was located in the boreal forest 35 km north of Haines Junction (61°N, 138°W) in southwestern Yukon Territory. Douglas (1974) classified the vegetation of the locality as a *P. glauca* – *Shepherdia canadensis* (closed phase) community. The growing season lasts from mid-May to mid-August (Turkington et al. 1998). Summer rainfall (May to August inclusive) in the area is both low and variable: it ranged from 50 to 146 mm, averaging 110 mm, with a coefficient of variation (CV) of 31% (data for Haines Junction, 1960–1999, are from the Canadian Meteorological Centre).

Three replicate sites separated from each other by at least 3 km were chosen. On each site, one control (C) grid and one treatment grid (T) grid were separated by 50–100 m. While C grids were subjected to natural rainfall only, T grids were supplemented with irrigation. All grids were staked at 14-m intervals; grids at sites 1 and 2 were staked in a 10 by 10 fashion (1.6 ha each) and grids at site 3 were staked in a 13 by 7 fashion (1.4 ha each). These six grids were used for the 5 years of experiments.

Table 1. Rainfall amounts (mm) between May 1 and August 31 at Haines Junction (near the experimental sites) during the 5 summers of experiments, as well as percent increases (2 m from each sprinkler) on treatment (T) grids compared with control grids.

Year	Control grids (mm rain)	Percent increase		
		T ₁	T ₂	T ₃
1995	110	47	56	51
1996*	110	47	67	67
1997	172	29	38	81
1998	49	198	143	380
1999	146	16	64	84

Note: Rainfall data were obtained from the Canadian Meteorological Centre.

*Rainfall data from May 1996 are missing.

On T grids, an irrigation system was built with PVC pipe, on which 17–23 rotating sprinklers were installed at 30-m intervals. Sprinklers were 1.5 m above ground. Water was fed to the irrigation system with an 8 HP gas-powered pump that took water from a nearby pond. Each sprinkler delivered water over a 14-m radius area at a rate of ca. 35.8 L/min. During the 5 summers of irrigation, the three T grids received between 23 and 186 mm more summer rainfall (average 81 mm) than controls (Table 1). Control rainfall was increased by 16–380% (average 91%) on the irrigated grids. The total amount of water received by the T grids during any experimental summer ranged between 82 and 214% (average 136%) of the maximal summer rainfall (146 mm) experienced in the region (data for Haines Junction, 1960–1999, from the Canadian Meteorological Centre). Irrigation generally occurred on three occasions on each T grid each year, generally starting around 15 June and ending around 7 August. This irrigation period overlaps the last two-thirds of the growing season.

Sampling procedures

All samples (mushrooms, plants, or invertebrates) were taken from stations distributed in a checkerboard pattern on

each grid. In 1995, sampling stations were located at grid stakes. However, on irrigated sites, sprinklers were not equally spaced from stakes, thus generating too much variability in the amount of water received at sampling stations. Therefore, from 1996 on, we positioned our sampling stations relative to sprinklers instead of stakes. For controls, sampling stations remained located relative to stakes. There were 23 sprinklers on T grids 1 and 2 and 17 on grid 3. Hence, 23 stations were sampled on each of T₁, T₂, C₁, and C₂ (the C grids being the corresponding control grids) and 17 stations on each of T₃ and C₃ from 1996 on, except when specified otherwise. The experimental units were grids. Similarly, if two quadrats were sampled per station, the sample was the average of the two quadrats, not the individual quadrats.

Mushroom biomass

To avoid destructive sampling of mushrooms, we first developed a predictive formula to calculate fresh biomass from their cap area. A small number (62) of mature mushrooms collected in August 1995 (away from sampling stations) were used to determine this relationship. Because mushroom caps were circular overall, we calculated cap area using the following formula: $\pi(0.5 \times \text{diameter})^2$. The cap diameter of each of these mushrooms was measured to the nearest 1 mm, while their mass was measured to the nearest 0.001 g. We did not distinguish species of mushrooms. Using this relationship, mushroom fresh biomass was determined on quadrats on each grid once a year, in August, from 1995 to 1999.

In 1995, mushrooms were monitored using 14 × 2 m quadrats ($n = 25\text{--}28$ per grid) laid between adjacent grid stakes. Mushrooms were divided among three size (cap diameter) classes, small (0–4 cm), medium (4–8 cm), and large (>8 cm), and counted. Biomass in 1995 was calculated assuming an average diameter of 2, 6, and 8 cm for the small, medium, and large class, respectively.

From 1996 to 1999, the yearly August mushroom surveys were carried out using 34–46 quadrats per grid. Two 10 × 2 m quadrats were laid, one on either side of each sprinkler. The diameter of all mushrooms encountered in quadrats during those surveys was measured to the nearest 5 mm. Fresh biomass of mushrooms during those years was calculated from their individual cap diameter using the predictive formula developed in 1995.

Understory vegetation

In 1995 and 1996, aboveground biomass of the understory vegetation was measured on clip-plots once a year. In mid-August 1995, 30–34 clip-plots of 20 × 20 cm were used on each grid. Samples were air-dried for 4 months, and two species, *Arctostaphylos uva-ursi* and *Linnaea borealis*, were independently weighed. The remaining species were weighed as one group. The clip-plots were larger in 1996 (30 × 30 cm) than in 1995, and were centered upon sprinklers ($n = 17\text{--}23$ per grid). Samples from August 1996 were oven-dried at 60°C for 4 days, sorted, and weighed according to eight categories (species or groups of species): grasses, *A. uva-ursi*, *Arctostaphylos rubra*, *L. borealis*, *Equisetum* spp., *Epilobium* spp., *Achillea millefolium*, and remaining species as one group.

From 1997 to 1999, only three species were monitored at 17–23 stations (sprinklers on treatments, and stakes for controls) per grid: *Festuca* sp., *Epilobium* sp., and *A. uva-ursi*.

For the first two, the total height of the four individuals closest to a station was measured as an index of growth. For *A. uva-ursi* (a perennial shrub), two branches per station, 10 mm from the terminal bud, were tagged in June 1997 and the additional growth was measured each August until 1999.

Berry production in *A. uva-ursi* was also monitored. In July 1996, 15 permanent quadrats of 30 × 30 cm were installed on each grid and all berries were removed from inside these quadrats because they had been produced in 1994 or 1995. Each quadrat was installed as near as possible to a sprinkler (or stake for C grids) in a patch of *A. uva-ursi* that was as dense as possible. From 1996 to 1999, all fruits in each quadrat were harvested and counted at the end of August. An additional two to four quadrats per grid were installed in 1997.

Spruce

White spruce growth was estimated once a year, during August, from 1995 to 1998 through the “relative lateral branch growth ratio” (LBG) (C.J. Krebs 1995, unpublished data). The terminal growth of a lateral branch during a given year is compared with its terminal growth during a previous standard year. This comparison corrects for the inherent growth rate of that branch because different trees and different branches within a tree have different growth rates. For example, LBG 1995 / LBG 1994 = 1.5 indicates that the branch grew 50% more in 1995 than in the pre-irrigation year (1994). One branch was sampled in two to four trees per sprinkler (or stakes for C grids), but trees less than 18 cm in circumference were excluded.

Invertebrates

Population indices for forest-floor invertebrates were obtained using pitfall traps in August 1995 and June 1996. For each trapping period, 16–25 pitfall traps of 9 cm diameter and 12 cm depth were set for 17–34 days. The number of traps and number of days of trapping were balanced for both the T and the C grids at each site. The pitfall traps were filled to a depth of 3 cm with a mixture of water, ethanol, and liquid soap. Invertebrates caught in traps were stored in 70% ethanol and identified later. Traps that were disturbed by animals or that dried during the trapping periods were not included in the analyses. The taxonomic groups monitored were terrestrial snails (Mollusca; Gastropoda), centipedes (Chilopoda), spiders (Arachnida; Araneida), grasshoppers and allied groups (Insecta; Orthoptera), ground beetles (Insecta; Carabidae), carrion beetles (Insecta; Silphidae), and hymenopteran and lepidopteran caterpillars combined. Other invertebrates were ignored because they were too rare. The number of individuals of each group per pitfall trap per day was calculated. The traps were installed 1 m from grid stakes in 1995 and within 3 m of sprinklers (or stakes for C grids) in 1996.

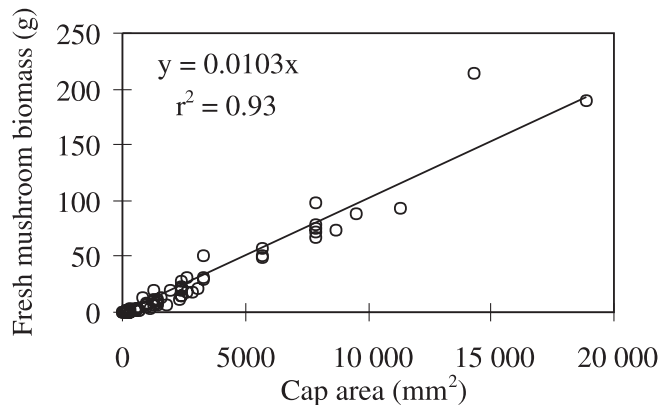
Voies

Voies were livetrapped with 50 Longworth traps per grid set at every other grid stake in a checkerboard pattern for the entire duration of this experiment. Traps were prebaited (with apple bits and oats) for 2 days prior to each trapping session. Trapping sessions lasted for 2.5 days, except during 1999, when the trapping session lasted only 1 night. Trapping sessions occurred twice each year from 1995 to 1998, once in

Table 2. Sample size per grid (n), average clip-plot dry biomass (g) per grid per group, within-grid standard deviation (SD), and non-parametric Kruskal–Wallis one-way ANOVA U and P values, in August 1995.

Group	C_1 ($n = 33$)		T_1 ($n = 33$)		C_2 ($n = 34$)		T_2 ($n = 33$)		C_3 ($n = 24$)		T_3 ($n = 26$)		U	P
	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD		
<i>A. uva-ursi</i>	6.2	8.7	6.1	8.2	1.2	2.6	5.6	7.6	3.0	4.0	2.3	3.2	4.0	0.83
<i>L. borealis</i>	0.1	0.5	0	0	0.1	0.4	0.6	1.1	0.6	1.0	0.3	0.7	5.0	0.83
Other	1.2	1.1	1.1	1.2	1.3	1.9	0.9	0.9	1.2	1.1	1.1	1.5	9.0	0.05
Total	7.5	8.6	7.2	8.5	2.5	3.4	7.1	8.0	4.9	4.0	3.7	3.6	4.0	0.83

Fig. 2. Linear relationship between individual fresh biomass calculated from 62 mushrooms collected in August 1995 and their respective cap areas.



June and once in August, to obtain seasonal population indices. In 1999, voles were trapped only once, in August. The minimum number of individuals known alive (MNA) (Krebs 1966) was used as the population index for each trapping session. Captured animals were individually identified to species, ear-tagged, and weighed, and sex and reproductive condition were determined before release. The reproductive condition of females was classified as (i) recently mated (vagina opening perforated or not); (ii) lactating; or (iii) near parturition (wide gap between pubic symphyses). Obviously pregnant females were also noted. The reproductive condition of males was classified as (i) scrotal or (ii) abdominal testes. The Animal Care Committee of The University of British Columbia approved the above procedures (protocol No. A97-0062).

Statistical analyses

When the data concerned multiple yearly surveys and did not depart from ANOVA assumptions, a three-way ANOVA (year \times site \times treatment) mixed model without replication was performed using grid averages. Year (number of levels according to number of yearly surveys) and treatment (two levels: irrigated or not) were fixed factors, while site (three levels) was random. If the data concerned a single yearly survey, a two-way ANOVA (site \times treatment) without replication was performed instead. If data departed widely from ANOVA assumptions and could not be corrected by log or square-root transformations, a non-parametric Kruskal–Wallis one-way ANOVA with replication was performed. Since several species of plants and invertebrates were monitored simultaneously, Bonferroni corrections for multiple comparisons

(according to the number of groups analyzed for) were applied to determine the appropriate P -value threshold of acceptance, and those are specified in the corresponding sections below. Statistical analyses were done using SYSTAT for Windows (Wilkinson 1991).

Results

Mushroom biomass

Fresh biomass of individual mushrooms was strongly correlated with cap area ($r^2 = 0.93$; Fig. 2). The regression equation obtained from this relationship was used to calculate fresh biomass per quadrat. No data were collected in 1998, as mushrooms were nearly absent, and 1998 was therefore excluded from the statistical analysis. For all other years, average biomass per quadrat was, on average, 250% greater on T grids than on their respective controls (Fig. 3a). Biomass on all grids was greatest in 1997. The three-way ANOVA (year \times site \times treatment) revealed that the treatment effect on mushroom biomass was statistically significant ($F_{[1,2]} = 63.0$, $P = 0.02$). Neither the year effect nor the interaction term (year \times treatment) was significant ($F_{[3,6]} = 3.2$, $P = 0.10$, and $F_{[3,6]} = 2.5$, $P = 0.15$, respectively).

Understory vegetation

Data on understory biomass from both 1995 and 1996 had to be analyzed with a non-parametric Kruskal–Wallis one-way ANOVA, since samples departed widely from ANOVA assumptions, even with log or square-root transformations (Tables 2 and 3). Also, since the statistical analysis concerned several species in both years, the P -value acceptance level had to be corrected for multiple comparisons. The acceptance level was $\alpha = 0.05/4 = 0.013$ (three species and total understory biomass) in 1995 and $\alpha = 0.05/9 = 0.01$ (eight species and total understory biomass) in 1996.

Irrigation had no significant effect on understory plant species or total understory biomass in both 1995 and 1996 at α levels of 0.013 and 0.01, respectively (Tables 2 and 3).

Both *Festuca* sp. and *Epilobium* sp. grew more in 1998 than in 1997 or 1999 (Figs. 3b and 3c), and the year effect was significant for both species ($F_{[2,4]} = 8.5$, $P = 0.04$, and $F_{[2,4]} = 10.5$, $P = 0.03$, respectively). In *A. uva-ursi* (Fig. 3d), the data had to be log-transformed to meet ANOVA assumptions, and growth was not statistically different from year to year ($F_{[2,4]} = 2.3$, $P = 0.22$). The treatment and year \times treatment effects were not significant for either species.

For the purpose of the statistical analysis, the data on berry production in *A. uva-ursi* from 1995 were excluded because of the large error involved in dating the berries, since they were collected in early summer 1996 and could have

Table 3. Sample size per grid (n), average clip-plot dry biomass (g) per grid per group, within-grid standard deviation, and non-parametric Kruskal–Wallis one-way ANOVA U and P values, in August 1996.

Group	C_1 ($n = 23$)		T_1 ($n = 23$)		C_2 ($n = 23$)		T_2 ($n = 23$)		C_3 ($n = 17$)		T_3 ($n = 17$)		U	P
	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD		
<i>A. uva-ursi</i>	4.3	5.4	8.3	10.0	3.3	7.3	5.0	6.5	4.3	7.2	7.6	11.2	0.0	0.05
<i>A. rubra</i>	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.3	2.0	2.3	0.6	1.5	4.5	1.00
Grass	1.4	1.2	1.3	1.3	1.0	0.9	1.5	1.3	0.4	0.4	0.7	0.9	3.0	0.51
<i>Equisetum</i> spp.	0.0	0.0	0.0	0.0	0.2	0.4	0.1	0.1	0.7	0.6	0.2	0.2	5.5	0.66
<i>Epilobium latifolia</i>	0.6	0.9	0.6	1.0	0.1	0.3	0.1	0.2	0.1	0.1	0.1	0.3	5.0	0.83
<i>A. millefolium</i>	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.2	4.5	1.00
<i>L. borealis</i>	0.1	0.6	0.0	0.0	0.5	1.1	0.4	1.0	1.0	1.7	0.5	0.8	7.0	0.28
Other	0.2	0.3	0.2	0.3	0.4	0.9	0.2	0.2	0.6	0.5	0.4	0.5	5.0	0.83
Total	6.7	5.9	10.4	9.4	5.5	7.9	7.3	6.9	9.0	7.1	10.2	11.6	1.0	0.13

Table 4. Average number of invertebrate per trap per day for each grid (in fall 1995 and spring 1996) using 16–25 pitfall traps for 17–34 days, together with three-way ANOVA F and P values for year, treatment, and year \times treatment interaction effects.

Year	Grid	Snails	Spiders	Centipedes	Grasshoppers	Carabidae	Silphidae	Lepidoptera	
1995	C_1	0.026	0.249	0.020	0.091	0.043	0.018	0.067	
	T_1	0.002	0.272	0.002	0.082	0.065	0.062	0.017	
	C_2	0.003	0.468	0.008	0.127	0.066	0.014	0.083	
	T_2	0.002	0.434	0.004	0.099	0.075	0.018	0.029	
	C_3	0.048	0.496	0.012	0.058	0.029	0.031	0.044	
	T_3	0.027	0.294	0.002	0.029	0.035	0.035	0.048	
1996	C_1	0.000	0.315	0.006	0.002	0.161	0.000	0.027	
	T_1	0.008	0.712	0.000	0.002	0.246	0.000	0.052	
	C_2	0.008	1.214	0.013	0.035	0.168	0.000	0.201	
	T_2	0.000	1.386	0.010	0.056	0.138	0.000	0.350	
	C_3	0.058	0.767	0.004	0.004	0.094	0.000	0.125	
	T_3	0.029	0.742	0.005	0.005	0.069	0.000	0.221	
Year									
		$F_{[1,2]}$	0.0	7.0	0.2	23.0	10.2	17.3	3.2
		P	0.88	0.12	0.71	0.04	0.09	0.05	0.22
Treatment									
		$F_{[1,2]}$	3.9	0.3	6.2	4.8	0.3	1.7	1.9
		P	0.19	0.62	0.13	0.16	0.65	0.32	0.30
Year \times treatment									
		$F_{[1,2]}$	0.2	16.9	5.2	6.4	0.0	1.7	9.4
		P	0.71	0.05	0.15	0.13	0.95	0.32	0.09

been from 1994 or 1995. The data from 1996–1999 had to be log-transformed to conform to ANOVA assumptions. Berry production was, on average, 150% higher on irrigated grids than on their respective controls (Fig. 3e), although this trend was not present in 1995 and 1997. Berry numbers were extremely low in 1997, while they were at their highest in 1998. Numbers were intermediate in 1996 and 1999. The three-way ANOVA on the data from 1996 on revealed the presence of a year effect ($F_{[3,6]} = 10.7$, $P = 0.01$), but neither the treatment nor the year \times treatment effect were significant ($F_{[3,6]} = 2.9$, $P = 0.13$, and $F_{[1,2]} = 8.5$, $P = 0.10$, respectively).

Spruce lateral branch growth

In general, spruce LBG from 1995 onwards was less than in 1994 (Fig. 3f). The three-way ANOVA showed the treatment effect to be not significant ($F_{[1,2]} = 0.7$, $P = 0.48$).

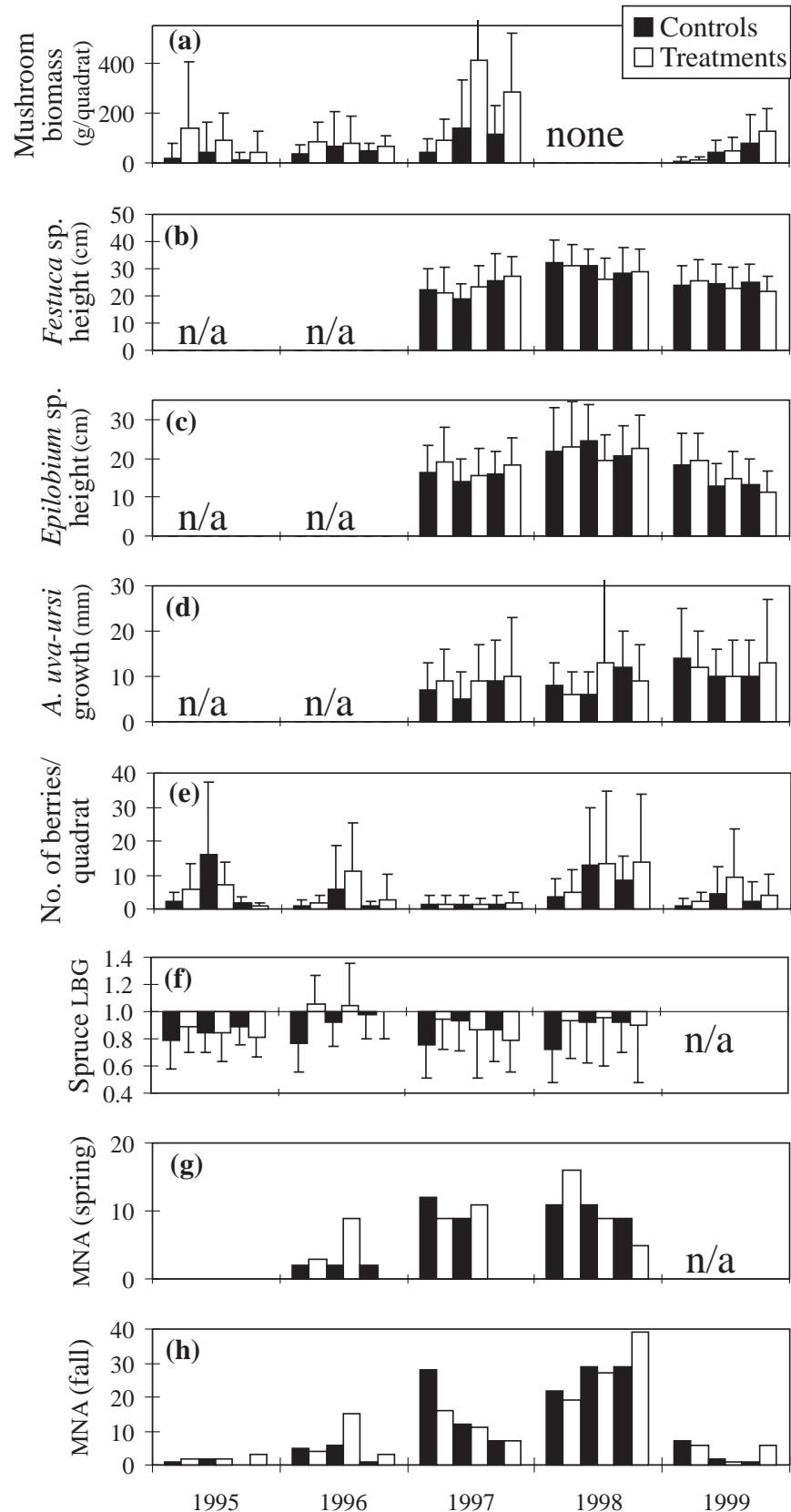
However, as in the case of understory vegetation, the year effect was significant ($F_{[3,6]} = 7.83$, $P = 0.01$), and for spruce LBG, so was the year \times treatment effect ($F_{[3,6]} = 10.6$, $P = 0.01$).

Overall, plant measurements that spanned at least 2 years and in which a year effect could be tested for using a three-way ANOVA showed this effect to be significant, except for growth of *A. uva-ursi*. Neither the understory vegetation species that were monitored nor spruce LBG showed a significant treatment effect.

Invertebrate numbers

The three-way ANOVA on invertebrates for 1995 and 1996 was performed on seven groups, hence the acceptance level was therefore $\alpha = 0.05/7 = 0.007$, as required by the Bonferroni correction. No significant effect of year, treatment, or year \times treatment interaction was found (Table 4).

Fig. 3. Time series (grid averages) of mushroom fresh biomass (a); *Festuca* sp. height (b); *Epilobium* sp. height (c); *A. uva-ursi* growth (d); numbers of *A. uva-ursi* berries per quadrat (e); spruce lateral branch growth ratio (LBG) (relative to 1994) (f); minimum number alive (MNA) per grid for *C. rutilus* in the spring (g); and MNA per grid for *C. rutilus* in the fall (h). Error bars show the standard deviation around the mean. Solid bars denote control (C) grids and open bars denote treatment (T) grids. The order of bars from left to right within any year and any time series is C₁, T₁, C₂, T₂, C₃, and T₃.



Vole numbers

Voies were absent on all grids at the beginning of the experiment in spring 1995, but increased consistently during both the spring and the fall until 1998 (Figs. 3g and 3h, respectively). Voies were scarce again in August 1999. In both June (1995–1998) and August (1995–1999), there was neither a significant treatment effect ($F_{[1,2]} = 0.1$, $P = 0.76$, and $F_{[1,2]} = 0.1$, $P = 0.80$, respectively) nor a year \times treatment effect ($F_{[3,6]} = 0.3$, $P = 0.82$, and $F_{[4,8]} = 0.3$, $P = 0.82$, respectively), but both showed a significant year effect ($F_{[3,6]} = 7.4$, $P = 0.01$, and $F_{[4,8]} = 10.4$, $P = 0.003$, respectively).

Discussion

The aim of this study was to test whether rainfall indirectly controlled densities of food-limited voies through its effect on food availability. We therefore tested the predictions that (i) the biomass of plants, mushrooms, and insects (food sources for voies) would increase as precipitation increased in the dry Kluane boreal forest, and (ii) food-limited voies would proliferate in response to this increase in food production. Although voies varied from being absent to being at high densities during the course of this 5-year study, their numbers remained unaffected by irrigation across the nine trapping sessions in both June and August. Because the irrigation levels on T grids ranged between 82 and 214% (average 136%) of the maximal summer rainfall experienced in that area between 1960 and 1999, voies should have shown a response to irrigation if variation in rainfall levels affects their densities. Their lack of response therefore signifies that rainfall does not affect vole densities through a bottom-up trophic chain.

If rainfall does not affect vole densities, it is either because food sources for voies are not limited by summer rainfall, or that vole numbers are not food-limited (even if their food is water-limited). The latter is unlikely, as both Gilbert and Krebs (1981) and Schweiger and Boutin (1995) generated population increases in this species in that area with food addition.

It is unlikely that the lack of vole response to irrigation followed from experimental discrepancies in population censuses, because both Schweiger and Boutin (1995) and Gilbert and Krebs (1981) obtained increases in vole density with food addition on grids of comparable sizes (1.8 and 2.3 ha, respectively) to ours (1.4 or 1.6 ha) and using similar census methods.

Conversely, it is more likely that food sources for voies are not water-limited in the Kluane region. In central Alaska, *C. rutilus* feeds on lichens, mushrooms, mosses, and dicot leaves, fruit, and seeds, as well as arthropods (West 1982). Among the food categories that were monitored in our experiment, only mushrooms responded to irrigation. West (1982) found mushrooms in the diet of *C. rutilus* in central Alaska, but only as a small fraction of the diet, i.e., 6, 2, and 1% during spring, summer, and fall, respectively. Fruit and seeds were eaten much more, representing 73, 62, and 92%, respectively, and arthropods constituted from <1 to 6% (West 1982). Although irrigation generated an increase in mushroom fresh biomass that averaged 2.5-fold (Fig. 3a) and reached as high as 7.4-fold between C₁ and T₁ in 1995, this did not affect vole densities. Thus, voies were not “mushroom-

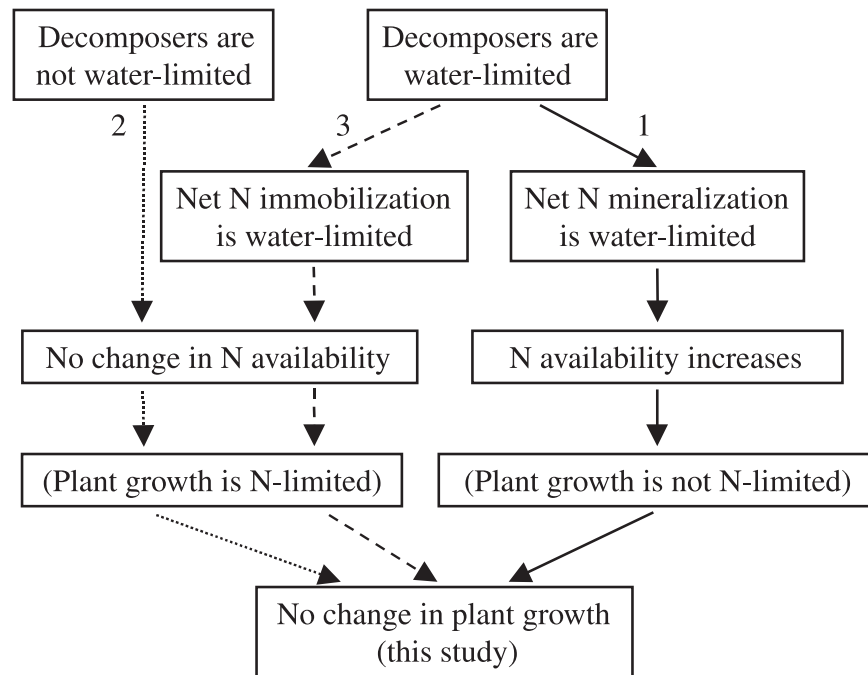
limited”, and any food limitation had to be in relation to other food, probably fruit and seeds because these represent the staple items of their diet. If fruit and seeds are the limiting food sources and did not react to irrigation, it is not surprising that the voies also showed no response. What is surprising is that only mushrooms were shown to be water-limited in the dry Kluane rain-shadow zone, and not the plants. Water deficits have been shown to substantially reduce growth in *Pinus taeda* and *Pinus echinata* (Basset 1964), so the reduction of the water deficit by irrigation was expected to increase plant growth. Therefore, it appears that plants are either stress-tolerant or limited by other factors.

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 these species is relieved, they do not respond by growing. This seems unlikely for some of the plant species found in the Kluane region, since nutrient additions in that area generated an increase in cover of *Festuca altaica*, *Mertensia paniculata*, and *A. millefolium*, as well as an increased growth rate in white spruce, *Salix glauca*, and *Betula glandulosa* (Turkington et al. 1998). Some plants in the Kluane area showed quick responses to nutrient-stress reduction, and are therefore not stress tolerators sensu Grime (1977). If plants in the Kluane region were water-stressed, their growth response to irrigation would have been noticeable.

Alternatively, vegetation in the Kluane boreal forest may be nitrogen-limited. Turkington et al. (1998) obtained an immediate response to fertilizer addition in the Kluane forest, and nitrogen limitation has been shown for the boreal forest in general (Zasada et al. 1977; Aronsson and Elowson 1980; Van Cleve and Alexander 1981; Bonan and Shugart 1989; Schulze et al. 1994). However, decomposition and nitrogen mineralization are known to depend on water availability (Meentemeyer 1978; Binkley et al. 1994). Decomposition in boreal forests is performed mostly by Fungi (Frontier and Pichod-Viale 1990), which also depend on soil humidity (Wilkins and Harris 1946). Mushrooms reacted strongly to irrigation and this suggests that nitrogen limitation in plants could have been alleviated by the treatment, assuming that mushroom biomass is indicative of the performance of decomposers and nitrogen mineralization. Thus, the idea that the lack of plant response to irrigation was due to nitrogen limitation and not water limitation seems discordant with the response of mushroom biomass to irrigation. This inconsistency can be resolved by confirming only one of the following three hypotheses (Fig. 4): hypothesis 1: plants in the Kluane region are not nitrogen-limited, therefore water-limited nitrogen mineralization by decomposers released unnecessary nitrogen with irrigation; hypothesis 2: plants in the Kluane region are nitrogen-limited, but decomposers are not water-limited and therefore could not have affected nitrogen availability in response to irrigation; hypothesis 3: plants in the Kluane region are nitrogen-limited and decomposers are water-limited, but in response to irrigation, decomposers immobilized nitrogen instead of mineralizing it. These hypotheses will be tested in subsequent publications (P. Carrier, in preparation).

Despite the fact that the Kluane boreal forest lies in a rain-shadow zone, its vegetation is clearly not water-limited. Nitrogen limitation is probably prevalent in the Kluane forest, as in boreal forests in general. However, mushroom

Fig. 4. Alternative ecological processes proposed to account for the lack of plant response to irrigation in the Kluane boreal forest and a summary of the predictions of hypothesis 1 (—), hypothesis 2 (·····), and hypothesis 3 (- - -).



biomass increased with irrigation in the Kluane forest and in turn should have increased nitrogen mineralization. Hence, irrigation should have reduced nitrogen limitation through its stimulation of decomposers. It is therefore unclear why plant production and vole numbers did not correlate with mushroom biomass on the irrigated sites. Soil nutrient status must hold the key to resolving this dilemma.

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