Ventilation in the subnivean tunnels of the voles Microtus agrestis and M. oeconomus

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Air exchange through the snow was examined under field conditions in northern Finland by measuring the temperature in air vents opened by voles (*Microtus agestis* and *M. oeconomus*) and by checking how CO_2 released under the snow spreads and disappears in the subnivean spaces. During freezing weather warm air was able to flow upwards along air vents for the first few hours only. Cold air flowing down from the snow surface into the air vent then stopped the flow. Opening of air vents did not depend on the CO_2 content under the snow cover. CO_2 did not accumulate under a dry snowpack at least 70 cm thick and not even wet snow 48 cm thick could suppress its disappearance. The highest CO_2 content measured under the intact snow cover was 0.25 vol. %.

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1. Introduction

For survival during the winter voles are dependent on the thermal insulation provided by snow (Johnson 1954, Pruitt 1957, 1959, Fuller et al. 1969). In fact, they spend nearly the whole winter in subnivean tunnels. Formozov (1961) measured the temperature in their air vents and found it to be higher than that in snow at the same depth. He concluded that air flowed continuously upwards along the vent. However, Bader et al. (1954) and Johnson (1954) both found that the direction of flow is sometimes reversed, cold air sinking down and displacing the warm air flow. Circulation of air may also occur through the snowpack. This phenomenon has usually been neglected by authors when discussing the overwintering of voles; in fact, emphasis has been laid on the stable temperature of the subnivean environment (Formozov 1946, Siivonen 1962, Pruitt 1970). According to Pruitt (1957), voles avoid any locally cold areas under the snow.

CO_2 that might accumulate in the subnivean spaces is said to be removed via the air vents (Formozov 1946, Baš enina 1956). In some places the CO_2 content in the subnivean spaces may be as high as 4 vol. % (Bašenina 1956), but according to Nekipelov (1958) and Kelley et al. (1967) it is usually almost the same as in air. Bader et al. (1954) found that acetylene was not able to penetrate the crust layers very well, but flowed along a layer of coarse-grained snow if there were no air passages through the snow cover.

As far as voles are concerned, the importance of the air diffusion through and within the snowpack has not been examined, and the necessity for extra ventilation is somewhat disputable. The purpose of this paper is to describe the ventilation in the subnivean spaces and the function of the air vents made by voles under field conditions.

2. Methods

This study was carried out at Kilpisjärvi (69°03′N, 20°49′E) in the winters of 1977 and 1979 and, in part, at Simo (65°37′N, 25°00′E) in winter 1977. Air flow was measured in 234 air vents by the method of Formozov (1961), and by analysing the spread and disappearance of CO_2 under the snowpack in 32 field experiments. In this study the term " air vent" is applied only to those holes dug by voles through the snowpack along which the voles do not emerge, as distinguished from those which these animals, especially species of *Clethrionomys*, use regularly for gaining access to the snow surface (Siivonen 1972). In order to identify the species concerned, voles were caught in traps inserted into the air vents.

CO_2 concentration under the intact snowpack was determined in four study areas at Kilpisjärvi during winters 1977 and 1979 from the beginning of January to the beginning of May. Each study area was 100 m^2 in size. Observations on the distribution of air vents of voles were made not only in the eight study areas at Kilpisjärvi but also in the four study areas (100 m^2 each) at Simo in December 1977. The CO_2 concentration was determined with a Scholander micro-gas analyser to the nearest 0.015 vol. % (Scholander 1947) and with a Dräger gas

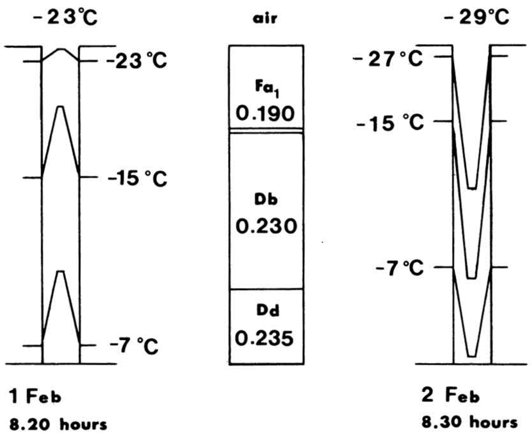

Fig. 1. Cooling of a new warm air vent during 24 h. Snow thickness 43 cm. Snow density and type are in the middle. Fa_1 = new, flake-like snow, grain diameter more than 1 mm, Db = old, fine-grained snow, grain diameter less than 2 mm, Dd = old coarse-grained snow, grain diameter more than 2 mm. (The diameter of the air vent was about 4 cm, and has not been drawn to scale).

analyser fitted with tubes Ch 30801 (0.01—0.3 vol. %) and Ch 23501 (0.1—1.2 vol. %). Because the analysers differed in accuracy the results are given to the nearest 0.01 vol. % when working with CO_2 concentrations in the range of 0.03—0.3 vol. %, but when the concentrations measured were higher the results are given only to the nearest 0.1 vol. %. Before an air sample was drawn into the Dräger analyser tube under field conditions it had to be warmed in a water bath. The volume of gas needed for the Scholander analyser was only about 5 ml, whereas for the Dräger it was 100—1 000 ml. To eliminate any difference possibly caused by the different methods, gas was always released under a large area, at least 50 m^2, and the first sample was not taken until 1 h later. The two methods were used simultaneously in winter 1979, and the readings were the same to the accuracy needed.

Temperatures were measured with a Wallac EP-400 thermistor or with thermocouples connected to a Honeywell electronik Y 153 recorder. When readings were taken to the nearest 0.5 °C they were idential with the two methods. Wind velocity was measured with a hot wire anemometer (Ilmonen).

Variation in the density and grain size of the snow cover during the winter is not described in detail in this context. Of course, many other factors that simultaneously affect the air flow were not studied, such as air pressure, liquid water in the snowpack, and vegetation. The examples given in this study may describe the situation in the subnivean spaces of voles under climatic conditions typical of Finland, where the snow thickness seldom exceeds 80 cm.

3. Results

3.1. Distribution of air vents

The voles (*Microtus agrestis* and *M. oeconomus*) dug air vents with diameters of 2—3 cm. They could dig these through a snowpack 80 cm thick. There were at most five air vents per 100 m^2 in the eight study areas (open swamp and natural meadow) at Kilpisjärvi in the winters of 1977 and 1979, but in the four study areas at Simo (unmown meadow) 18 air vents per 100 m^2 were found in December 1977. Although there were no air vents in some areas during the winter, hay straws gnawed by voles were found in May when the snow had melted. Thus absence of air vents could not be equated with absence of voles. In most study areas the voles showed no haste to re-open holes that had been filled with snow. The number of air vents was not constant during the winter in any area. Even during the hardest frost (—44 °C), voles spent short periods of time at the openings of their air vents near to the cold snow surface.

3.2. Air flow through air vents and snowpack

The air vents in the study areas were mostly colder than the surrounding snow layer, showing that cold air from the snow surface had flowed downwards. When an air vent was opened during cold weather the warm air from the subnivean spaces could flow upwards for only a short period (Fig. 1). Hoarfrost at the openings indicated the upward flow of warm moist air. In relation to all vents found, such warm air vents formed only 5 % (7/162) at Kilpisjärvi (6 Jan — 3 May 1977) and 20 % (15/72) (December) at Simo. Snow depth was 35—80 cm at Kilpisjärvi and 25—35 cm at Simo. The downward flow of cold air through the air vent lowered the temperature at the bottom of the hole by many degrees below that under the intact snow cover (Table 1). Possibly, a plug of cold air suppresses air flow in either direction.

Table 1. Examples of temperatures at the bottom of cold and warm air vents of voles.

Temperature °C			Snow depth	Density of snowpack
Bottom	Air	Ground surface under intact snow	cm	g/cm³
—15	—37	—5	55	0.230
—15	—28	—5	42	0.220
—24	—26	—6	30	0.170
—12	—25	—4	65	0.220
— 6	—12	—3	70	0.240
— 3	—40	—3	55	0.210
— 3	—21	—2	45	0.220
— 3	—16	—3	68	0.305
— 4	— 4	—4	55	0.310
0	+ 2	0	58	0.310

Table 2. Examples of disappearance of CO_2 released under snow in areas at Kilpisjärvi in 1979.

Time in which CO_2 disappeared (h)	Mean temperature (°C) Air	Ground surface	Snow depth cm	Wind speed m/s
13.0	−27	−4	57	—
7.0	−14	−3	55	—
9.0	−15	−3	55	—
3.0	− 6	−4	55	1.5
4.5	− 5	−3	72	0.3
3.0	− 5	−3	42	0.3
4.5	+ 8	0	29	—
4.0	+ 8	0	28	—

When the temperature gradient between the air and the ground surface became small it was not possible to show the direction of air flow by measuring the temperature difference.

When CO_2 was released into the subnivean spaces it disappeared, although there were no air vents or other holes in the snow. Such ventilation was not dependent on the temperature gradient, and diffusion occurred without such a gradient or even against it, even in wet show (Table 2). Not even hard snow suppressed the disappearance of CO_2, as shown by the following experiment. CO_2 was released under a winter road 4 m broad where the snow was compressed. The air temperature was 8 °C and the snow thickness 39 cm. There was no wind. The gas, the original concentration of which was 0.30 %, disappeared within 5 h. When CO_2 was released under a snow cover 70 cm thick in the middle of a steep slope (about 55 %), during 1 h the gas spread could be traced about 2 m downhill and only 0.5 m uphill. The air temperature was — 5 °C and there was no wind. On flat ground the spread of CO_2 could not be followed farther than 0.5—1.5 m under the same conditions.

3.3. CO_2 content under intact snow

The CO_2 concentrations measured under snow at Kilpisjärvi were never high enough to have any physiological effects on voles. At its highest the concentration rose to 0.27 %. This value was measured in an unmown meadow only on 3 days in the beginning of May 1977 during a warm spell (3—8 °C) when the whole snowpack was melting and wet throughout. During the winter and in spring 1979 the CO_2 content was nearly always close to that of air.

4. Discussion

The outflow of warm air through an air vent is probably always of quite short duration. The direction of flow will be reversed as soon as the pressure of cool, heavy air overcomes the buoyancy forces of the warm air in the air vent. Determination of this point was not possible in this study. An upward flow of warm air could occur only when the air vent was connected with large undersnow spaces, so that the outflowing air could be replaced by new warm air. The analogy between chimneys and air vents presented by Formozov (1961) is relevant in this respect, too. Cooling of the air vent continues during cold weather until the vent is filled with cold air. Of course, cooling is greatest in early winter, when the snow cover is thin.

Continuously used air vents may bring the voles in their undersnow tunnels into closer contact with the supranivean environment. Variations in thawing and cold spells during the winter are, perhaps, not such distant events for them as has usually been supposed (Pruitt 1957, Folk 1974:342). A small temperature drop in the subnivean spaces may not be harmful to the voles. At temperatures below the melting point food conservation is improved (Irving 1972:45). Low temperatures also reduce the production of CO_2 by decaying litter. A drop of only 1 °C below freezing point would be sufficient.

Although the air flow through air vents carried away CO_2, ventilation was not dependent on it. Obviously, CO_2 could diffuse along its concentration gradient and against the temperature gradient. Locally produced CO_2 also spreads not only through the snowpack but along the subnivean spaces. In most parts of Finland the snow cover is thin enough throughout most of the winter to permit effective ventilation. Liquid water in snow may transport or dissolve CO_2. As far as I know, this phenomenon has not been examined. During the winter, as a result of metamorphism of the snowpack, the subnivean spaces become larger (Mellor 1964). This increase in the air permeability of snow facilitates horizontal gas flow. In places where the snow cover is penetrated by trees and bushes, ventilation in the subnivean spaces and tunnels will usually be even more effective than in the areas described in this study. The examples given here of the time in which CO_2 disappeared from the subnivean spaces are in certain respects maximal estimates. Without discussing what induces the voles to make air vents, we may note that this behaviour is not necessary for reducing the CO_2 content in their subnivean tunnels.

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