

IN SITU CARBON DIOXIDE FLUX FROM ARCTIC TUNDRA
DURING FREEZE-UP

by

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INTRODUCTION

It has been hypothesized that microbiological activity of tundra microorganisms is restricted by the harsh environmental conditions. Consequently the slow decomposition of organic matter and debris limits nutrient recycling in tundra. These nutrient deficiencies in turn may be one of the rate limiting parameters in regulating the production of fauna and flora in the ecosystem. It was demonstrated by a number of investigators at different circumpolar sites during the International Biological Program that decomposition is not limited per se by a low decomposer biomass (26). The slow decomposition reported in tundra may be caused by: high soil carbon/nitrogen ratios, limited aeration, low levels of inorganic nutrients, short annual period of above freezing temperatures, and generally low temperatures.

Since CO_2 is the major end product of decomposer metabolism, field measurements of CO_2 flux represent a convenient indication of the decomposition processes in the system. The pioneering paper of Douglas and Tedrow was one of the first attempts to measure decomposition rates in tundra (4). This study was conducted in the vicinity of the Arctic Research Laboratory near Barrow, Alaska which has been a focus for tundra research since the 1950's. During the International Biological Program (IBP) in 1973, Peterson and Billings determined the rate of CO_2 flux from tundra at Barrow during the summer months using the infrared technique in a darkened chamber (12). Concurrently Coyne and Kelly used an aerodynamic method to estimate CO_2 flux (2), and Benoit used an in situ CO_2 alkali absorption method on one of the IBP sites where differ-

ent habitats expressed in polygon ground development were investigated (1). The CO_2 alkali absorption method permitted extensive replication on each habitat over the extremely heterogenous tundra at a reasonable cost where electrical power was not available. The habitats varied from moderately productive to very barren. These habitats develop several meters apart horizontally and centimeters apart vertically by thousands of years of annual freeze-thaw cycles. Benoit measured the CO_2 flux from undisturbed cores in the different habitats on a rotation system from the period of late June to early September 1973. This method measured the net CO_2 flux from all the biological components in the system, therefore, the contributions of the individual components must be estimated by other methods, which are probably not possible at present. However, one perturbation which featured stripping of flora attempted to crudely estimate the decomposer vs. primary producer contribution to the CO_2 flux.

No investigations have measured the CO_2 flux of tundra during the early winter freeze-up period. Tundra soil may remain at 0 C for an extended period of time in early winter when the air temperatures are below 0 C because tundra is acting as a heat sink. When the heat is dissipated the soil temperatures decrease in response to the cold air temperatures. The freezing point of soil water adsorbed on soil colloids will be lower than 0 C, and some microorganisms have metabolic activity between 0 C and -7 C under laboratory conditions (11). These two observations provide a theoretical rationale for predicting the synthesis of significant quantities of CO_2 from tundra microorganisms during freeze-up. It was the objective of this work to measure CO_2

output as a function of soil temperature during the freeze-up period under field conditions using the same undisturbed cores at the Barrow IBP site investigated by Benoit the previous summer. The formation of ice crystals in some cells of plants, animals and microorganisms will cause the death of the cells and thereby increase the pool of dissolved organic matter which some microorganisms may use for metabolism. The large quantities of CO₂ observed being produced under tundra snow cover by Kelly during parts of the winter provides indirect evidence that microorganisms are active at subzero celsius (8).

METHODS AND MATERIALS

Site Description

The experimental site was located on the International Biological Program Intensive Site near Barrow, Alaska. These soils have been described by Gersper (5) as highly organic with an elevated C/N ratio, acidic, high moisture content, low redox potential and consisting of a complex of Pergelic Cryosaprists, Histic Pergelic Cryaquepts, and Pergelic Cryosaprists with a thin histic horizon overlying a silty clay loam mineral horizon. The habitats examined included: flat centered wet meadow (plot 206 - 1973 data only), polygon trough (plot 440), polygon ridge (plot 441), and polygon basin (plot 442). The wet meadow site had a moss sedge vegetation with a minimum development of surface polygon features; this habitat was more uniform from the standpoint of plant standing crop and soil features than the habitats in the well-developed polygon study area. The polygon trough had a plant canopy which was similar to the wet meadow, but the soil was wetter and the soil profile was variable because of the intense effects of freeze-thaw cycles. The polygon ridge was well drained, had a high organic matter content and a moss-lichen cover dominated the soil surface. The polygon basin was poorly drained, high in organic matter, and the vegetation consisted of a sparse lichen cover.

The microbial characteristics of the decomposers have been described by Benoit (1) and Harris (7).

CO₂ Assay Procedure

CO₂ was collected in situ from the soil surface of 15 cm diameter cores. The PVC cores were 0.5 cm in thickness. Each core extended

approximately 3 cm above the soil surface and 4 cm below the soil surface. Each core remained in place after installation for a two year period. There were some discontinuities in the data of the polygon troughs due to flooding. In several cases, during the second year of the study some trough cores were relocated to drier sites; otherwise the replication would be reduced.

A modification of the alkali absorption technique was used. This method was used because reliable power sources were not available on the well-developed polygon site and this method permitted extensive replication under a variety of conditions in a variety of habitats. Five ml of standardized 0.1N NaOH solution was prepared in the laboratory and carefully carried to the field in screw cap culture tubes. The alkali was distributed in 3 cm diameter plastic culture dishes which were placed on the soil surface. The cores were sealed with parafilm and a plexiglass cover (31 cm square) which had a black opaque top was placed on top of each core. CO₂ was collected over a 24 hr period. In several cases extreme weather conditions prohibited sample collection for 48 hrs. These cases occurred during the coldest period of the study when activity was low. It was also necessary during the colder periods of this study to add NaCl to the alkali before standardization to lower its freezing point. The alkali from each plastic culture dish was returned to the same screw cap tube which had been used to transport it to the field. Distilled water was used to rinse the alkali from each dish. The alkali was collected at midnight during the summer 1973 season and 8 am during the fall-winter 1974 season. The midnight change was the closest hour to the daily minimum soil tempera-

ture reading which was administratively feasible. The 8 A.M. change during 1974 was chosen for a similar reason, except the safety of field personnel during adverse weather conditions was an additional factor. Six cores were used to sample each habitat each day. A sufficient number of cores were placed in the habitat study areas to permit each core to be sampled every fourth day. In the interim the core was 'in equilibrium' with the environment. A random number table was used to pick the set of cores for the original sample dates. Subsequent samples used the same cores on the same date. Daily triplicate controls were used in the field to determine the amount of CO_2 contributed by the atmosphere. Each control consisted of a core sealed at both ends with parafilm and covered by plexiglass. The controls were placed on a plywood board which was located at ground level. All alkali tubes were returned to the laboratory and immediately titrated with standardized 0.1N HCl to an endpoint using phenolphthalein. A 5 ml microburet was used for the analysis. The CO_2 absorption values were reported as $\text{mg CO}_2/\text{m}^2$ of soil surface. The method of Stozky (16) was used to calculate these values.

This method produced a value which estimates the net output of CO_2 from the soil-plant system and does not discriminate between producers and decomposers. The living and standing dead portion of the plant canopy in addition to the litter were removed from an additional series of cores in the polygon basin and polygon ridge habitats. Although a substantial portion of the surface decomposers were also removed by this stripping of the soil surface, this perturbation was designed to estimate what the remaining decomposer population could produce in CO_2 output.

A subset of the stripped cores were treated with 0.1167 g of Na_2HPO_4 /core which represented 150 lbs of phosphorus/acre. This treatment was designed to test the hypothesis that the extremely low phosphorus levels limit microbial growth and activity.

Soil temperatures represent average daily values obtained from thermistors sampled at three-hour intervals by a Grant recorder. The values obtained from the 5 cm depth were reported. Air temperature data was obtained from the United States Weather Bureau at Barrow, Alaska.

The data was analyzed statistically by use of the Scheffe Analysis of Variance test at the 5% confidence level (14). This test performed a multiple comparison of treatments resulting in significant subsets at the 5% level (the significant subsets are given in the Appendix Tables II, IV, and VI).

RESULTS

The rate and time which the tundra freezes is subject to considerable variation as a function of abiotic events. Light frosts are often observed during August. Freezing conditions become more frequent during September when the average daily minimum, maximum and mean air temperatures at Barrow Weather Station are -2.7 , 0.7 and -0.9 C respectively. The freezing process becomes intensive during October when the average daily minimum, maximum and mean air temperatures are -12.0 , -7.4 and -9.3 C respectively (17). This study was initiated during an unseasonably warm period in late August 1974 and was terminated when the soil was extensively frozen on 19 October. The soil temperatures at the 5 cm depth at the study area during this period are shown in Figure 1 (the data are given in the Appendix Table VII). The soil temperatures at the start of the study were unusually warm. Soil temperatures approached 10 C briefly during mid-summer in 1973, and were approximately 3 C during the late August - early September period. The break in the temperature data for 1974 shown by the dotted line in Figure 1 was due to a mechanical malfunction of the recorder which coincided with a drop to seasonal temperatures. The soil temperatures dropped after the warm period and remained relatively constant during the first twenty days of September at 2 to 3 C. For the next 20 days the soil temperature remained slightly above 0 C which corresponded to the "zero window" period. The soil temperature then dropped quickly after October 7 to temperatures less than -5 C. During the latter period it was often difficult to locate the experimental area because the

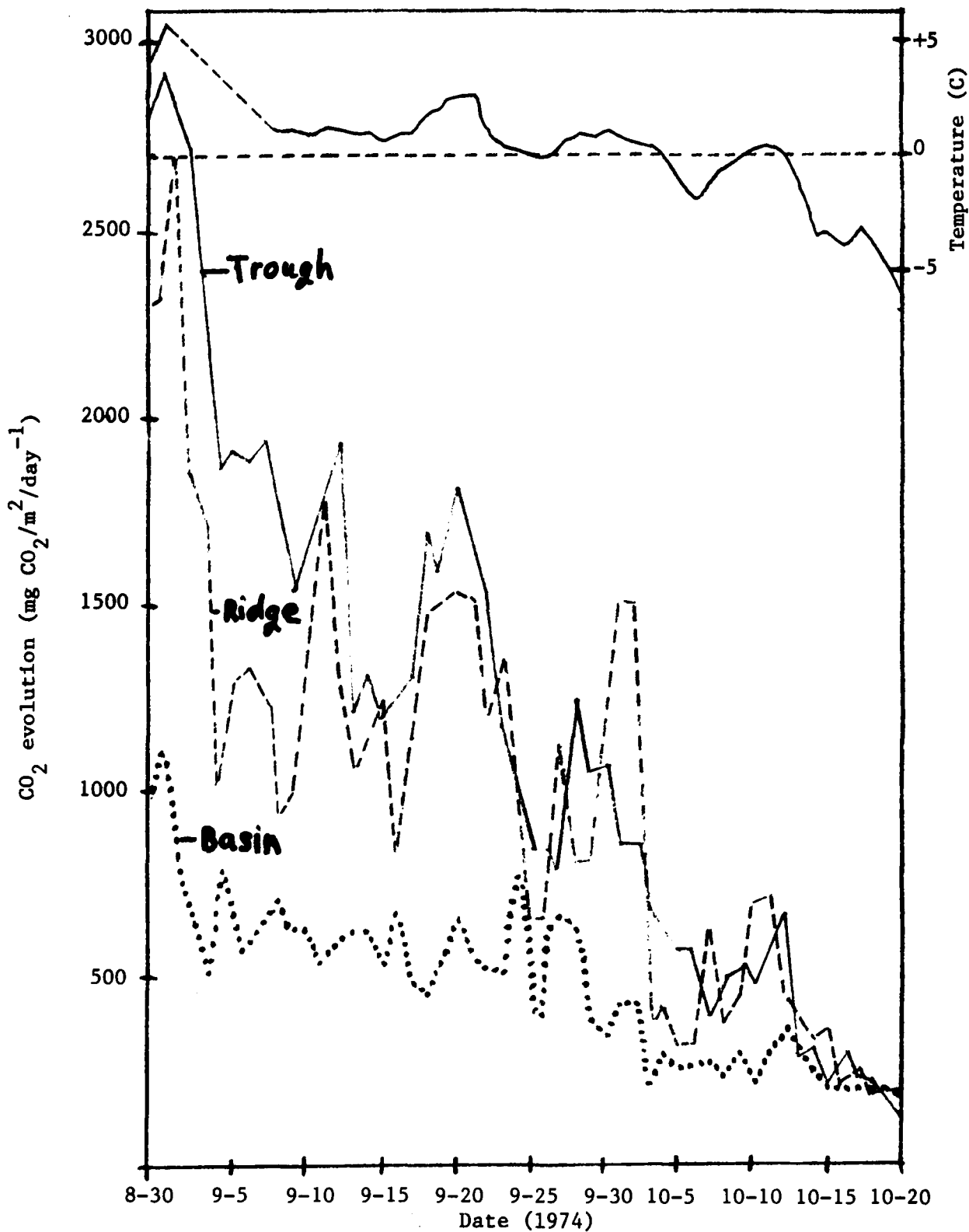


Figure I. Daily CO₂ evolution from polygon trough, ridge and basin habitats on tundra during freeze-up 1974 with 5 cm depth soil temperature shown as daily mean temperature, at IBP site 4, Barrow, Alaska.

cores were often completely covered by snow. The basin and trough cores were particularly difficult to locate. NaCl was used to lower the freezing point of the NaOH. Near the end of the experiment the alkali would freeze during the field incubation especially in the ridge habitat. Furthermore it was more difficult to seal the core at low temperatures. Under conditions of subfreezing temperatures and blowing snow, the quantitative recovery of the NaOH from the core was difficult.

The CO₂ daily averages for the three habitats on the Barrow IBP site 4 are also shown in Figure I. The CO₂ production from the trough, ridge and basin at the start of the study when soil temperatures were near 10 C were approximately 2900, 2300 and 1100 mg CO₂/m²/day on 31 August and 1 September. These values were greater than any other value obtained from the identical cores the previous year. When the soil temperature decreased radically on 2 September to a plateau near 2 to 3 C, the CO₂ production from the trough, ridge and basin dropped approximately 35, 40 and 45 percent respectively from the 1 September maxima. During the three day warming trend at the end of the plateau, there was an increased CO₂ level from the trough and ridge habitats, but not the basin. When the soil temperature dropped into the "zero window" phase from September 23 to October 6, the trough, ridge and basin CO₂ production dropped 70, 57 and 64 percent from the 1 September maxima. When the soil temperature decreased several degrees below 0 C on 3 October with the onset of a cold period, CO₂ declined but continued in the trough, ridge and basin to levels 17, 26, 22 percent that of the 1 September maxima. With the onset of deep winter conditions when the soil temperatures dropped below -5 C on 14 October, the CO₂ release con-

tinued in all three habitats at levels of approximately $150 \text{ mg CO}_2/\text{m}^2/\text{day}$ which corresponds to 5, 7 and 14 percent of the values observed during the warm period on 1 September. Five day mean values of the CO_2 flux are shown in Figure 2. A comparison of daily vs 5 day means illustrates the considerable variation caused by variations in temperature, wind velocity, moisture and snow cover.

It may be concluded from these data that CO_2 production from tundra decreases as soil temperature decreases, but the decrease appears to be an asymptote rather than a sharp extinction point as the system freezes. Most of the variation in CO_2 evolution could be accounted for by variations in the daily soil temperature. A multiple regression comparing CO_2 evolution rates of the three habitats with temperature accounted for 72% of the overall variation in the data. Correlation coefficients between individual habitats and temperature were also determined and the relationship between CO_2 evolution and soil temperature was observed. The regression equation for predicting temperature was: $\text{Temperature} = 4.67054 + (0.00263) \text{ basin} + (0.00180) \text{ trough} + (0.00223) \text{ ridge}$.

The Scheffe Analysis of Variance test was used to compare differences of CO_2 evolution in the three habitats at the 5% confidence level (14). The ridge and trough were different 22% of the days tested. The ridge is not as productive a habitat as the trough, but when conditions of temperature and moisture are favorable decomposition on the ridge can be significant. The ridge was consistently less than the trough (Fig. II) during early September when moisture may have been less available on the ridge than the trough. When moisture was adequate in late September and early October, the quantities of CO_2 evolved were very similar. The

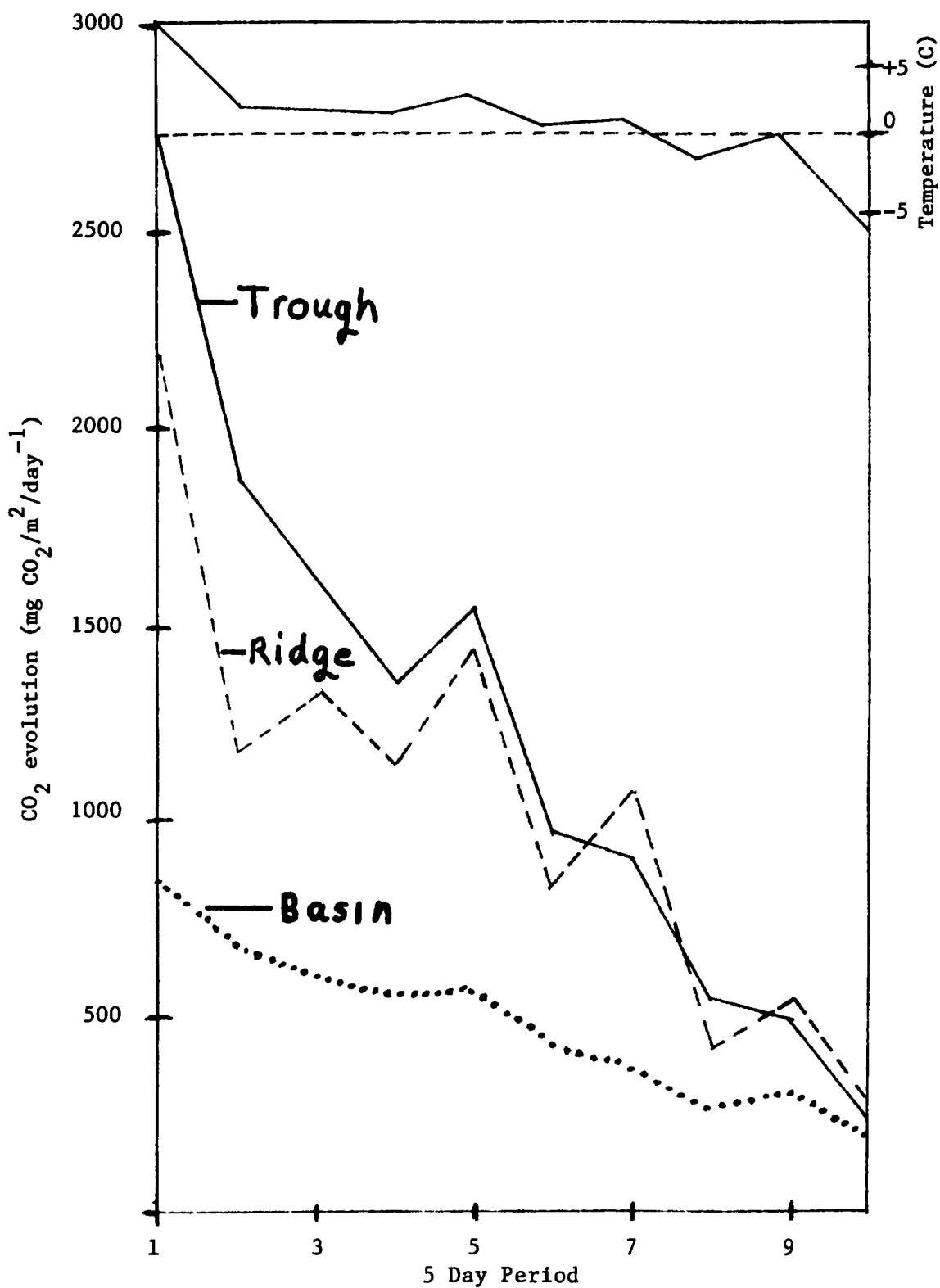


Figure II. CO₂ evolution from polygon trough, ridge and basin habitats on tundra reported as 5 day means during freeze-up 1974 with 5 cm depth soil temperature shown as 5 day means at IBP site 4, Barrow, Alaska.

basin was significantly different than the trough and ridge on 68 and 42% of the days tested respectively. These data are consistent with differences observed during the 1973 season. The very low CO₂ flux recovered from all three habitats coupled with the increased variation between cores within habitats during the coldest period reduced the number of times the habitats were significantly different in contrast to the 1973 summer period.

The CO₂ flux from the ridge and basin which had the litter and above ground live material removed are given in the Appendix Tables III and V. During the entire period of this study the stripped ridge and basin habitats were significantly different from the unstripped habitats 9 and 23 percent of the time respectively (Table I). Removing the surface layer removes much of the substrate which is readily available to microorganisms and exposes the more recalcitrant organic matter. This perturbation demonstrated that a very high percent of CO₂ flux from tundra surface can originate from microbial degradation of organic matter. This perturbation only shows the potential for decomposition because the surface canopy has an important regulatory effect on the decomposition of the soil organic matter. Mechanical and temperature perturbation of the tundra at Barrow demonstrates that destruction of plant canopy usually stimulates decomposition (1) and the addition of phosphorous did not increase the decomposition during a two year period although the level of available phosphorous was extremely low. The iron content of tundra was very high and apparently the phosphorous was rapidly complexed into iron phosphates in which the phosphorous was only slowly available to microorganisms and plants in the system.

TABLE I

time differences
were significant vs.
total number of ob-
servations.

| Treatments | | Percent |
|---|-------|---------|
| Basin/Ridge | 21/50 | 42% |
| Basin/Trough | 34/50 | 68% |
| Ridge/Trough | 11/50 | 22% |
| Basin/Basin No canopy w/PO ₄ | 6/22 | 27% |
| Basin/Basin No canopy/No canopy w/PO ₄ / w/o PO ₄ | 0/22 | 0% |
| Basin/Basin No canopy w/o PO ₄ | 5/22 | 23% |
| Ridge/Ridge No canopy w/PO ₄ | 1/22 | 5% |
| Ridge/Ridge No canopy/No canopy w/ PO ₄ /w/o PO ₄ | 0/22 | 0% |
| Ridge/Ridge No canopy w/o PO ₄ | 2/22 | 9% |

Significant Differences: CO₂ flux differences between different habitats or treatments on IBP Site 4, Barrow, Alaska during the 1974 freeze-up at the 5% confidence level.

The tundra is an extremely heterogenous soil system. The high standard deviation between cores within a habitat is evidence for the diversity in substrate, levels of nutrients and differences in the geometry of the matrix in the soil profile. When a fungus developed a fruiting body inside one of the cores of the stripped ridge treatment on 4 September 1974, the level of CO₂ flux was 271 percent greater than the other cores in the treatment.

DISCUSSION

If temperature is one of the major limiting parameters of decomposition than the usually warm soil temperatures observed at the start of this study should have stimulated CO₂ production. In fact, the observed CO₂ production values from the trough, ridge, and basin habitats during this warm period were greater than any value observed during the previous summer on the same sites. The trough, ridge and basin habitats produced CO₂ values of 2925, 2715 and 1102 mg CO₂/m²/day respectively. Since the trough produced the greatest quantity of substrate for decomposer activity higher CO₂ flux values on that habitat were expected. A good correlation ($r = 0.813$) between CO₂ production and soil temperature was observed in the trough. When the trough became water logged the CO₂ production was depressed even when temperatures were favorable. A marked depression in CO₂ production in the trough was observed the previous summer during an extremely wet period in early August. There was a high biomass of bacteria and fungi on the trough habitat with the fungi located primarily at the soil surface. A good correlation ($r = 0.794$) was also obtained between the soil temperature and ridge CO₂ production. On this habitat such positive correlation was less favorable. The fungi appear to dominate the decomposer biomass of the ridge habitat. The poorest correlation between soil temperature and CO₂ production was obtained on the basin habitat ($r = 0.723$). The basin remains a decomposer enigma. There was very little primary production on this habitat and there was very little decomposition although there were high quantities of organic matter. A

combination of poor aeration, high quantity of recalcitrant molecules, low inorganic nutrient status (especially phosphorous) and the soil matrix may insure stagnant gas and moisture conditions. The biomass of bacteria and fungi was much lower on this habitat than any other soil habitat on the Barrow site.

The CO₂ flux values observed from tundra under the most favorable conditions in this study were considerably lower than those obtained in low latitude ecosystems. Schultz used an in situ CO₂ absorption technique in which above ground plant parts had been removed to demonstrate that soil respiration rates in tropical soils varied between 300 and 2500 mg CO₂/m²/hr (15). The lowest value observed in this study was observed in a soil under drought and high temperature (42 C) conditions. Wanner measured CO₂ production in East Asian rain forest using methods similar to the technique used in this study and he observed rates between 120 - 300 mg CO₂/m²/hr (20). The high values obtained by Schultz may represent an extremely productive habitat or the clipping of the above ground parts may have stimulated soil and root respiration. Temperate zone values of 450, 220 and 1000 mg CO₂/m²/hr were observed on Missouri tall grass prairies (9), Tennessee oak forest (25), Minnesota forest (13) respectively.

The CO₂ values reported in this study represent the combined effect of soil fauna and flora. It is difficult, if not impossible at present, to measure the contribution of the individual components in the field. An unknown portion of the CO₂ collected in this study was CO₂ derived from respiration of above ground plant parts. Peterson and Billings

claim that about one third of CO_2 from the trough habitat originates from above ground plant parts (12). During the freeze-up period when air temperatures are less than soil temperatures, the above ground CO_2 respiration component should decrease relative to below ground respiration output (2). Tundra plants have large root/shoot ratios (3) and therefore root respiration can be a large portion of below ground CO_2 output. MacFadyen has summarized the various estimations of soil and root respiration and he estimated that 15 - 50 percent of the soil respiration can be attributed to roots (10). The lower values were observed in forest ecosystems, whereas the upper values reflected grassland ecosystems. Kucera and Kirkham (9) examined tall grass prairie soil and concluded that 60 percent was produced by microbial components and the balance was attributed to root respiration. In their investigation a large part of the below ground CO_2 production in the trough habitat was probably produced by the root component. Since the ridge and basin habitats have a very limited root component because lichens and mosses dominate the flora, the soil microorganisms probably contribute a larger percent of the below ground CO_2 flux than was observed in the trough. When the plant components were stripped from the ridge and basin habitats, the CO_2 flux was only reduced by 9 percent in the ridge and 23 percent in the basin. These values represent a conservative estimate of the microbiological decomposition because the removal of the plant material also removed a significant portion of the soil microorganisms. Many of the estimates of soil decomposition vs. plant respiration do not consider the rhizosphere. Implicitly, many investigators consider the rhizosphere microorganisms as part of the plant root. Dur-

ing the freeze-up period there may be more root exudation and sloughing of plant cells in response to mechanical damage due to freezing and rhizosphere microorganisms may have more readily available energy sources released than is available during mid-summer. The soil layer of tundra will freeze from the permafrost up and from the surface down, therefore, the 15 cm soil depth may be the last portion of the system to freeze and as the freeze-up progresses a larger component of the CO₂ flux may be due to soil microorganisms than to plants.

Different methods used to determine CO₂ flux may produce different values. The alkali absorption method may underestimate CO₂ flux because of the lack of air turbulence in the test chamber, formation of artificial convection layers through temperature changes within the absorption chamber and changes in CO₂ diffusion rates caused by changes in the alkali during the test period (15). Haber noted that the alkali absorption technique could absorb 75 ± 4.65 percent of the CO₂ released in a defined chemical system (6). Kucera and Kirkham compared the relative recovery of CO₂ from the alkali absorption and infrared techniques on subsamples of the same field soils. The alkali absorption technique CO₂ flux values were 61.3% less than that observed by infrared analysis (9). The infrared technique requires the transmission of gas through the collection chamber and consequently CO₂ may be "pumped" out of the test system. The infrared method may overestimate the precise flux value but the criticism that the alkali absorption method underestimates the precise value is probably also valid. The comparable values of CO₂ from wet meadow by Peterson and Billings (12) and the alkali absorption

method by Benoit (1) on the same dates on a similar soil at Barrow indicate the two methods gave similar results at lower temperatures, but the infrared method was more efficient in recovering CO₂ during the period when soil temperatures were at the seasonal maximum.

A close relation between soil temperature and CO₂ flux has been observed by numerous investigators (4,8,9,13,19,21,22,23,24). In this investigation a close relationship between soil temperature and CO₂ flux between the range of 10 C and -7 C was noted. Van Cleve and Sprague used the differential respirometer technique to measure respiration of Alaskan Boreal forest soil and observed zero respiration between the range of 1 and 5 C (19). Wiant noted that CO₂ production from Connecticut soil followed a Q₁₀ of 2 between the temperatures of 20 to 40 C using an infrared gas analyzer (21). However, he was not able to detect any CO₂ production at 10 C. CO₂ flux from an in situ Missouri soil was determined using the infrared technique and noted a marked seasonal effect (9). The winter values of this Missouri study were equal to the maximum values obtained from tundra in this study. Wildung et al. used the alkali absorption technique to measure CO₂ flux during a two year period of soil from arid shrub-steppe (22). The winter values in this Washington state study showed lower CO₂ flux at 1 C than was observed at Barrow in this study at 1 C. However, the maximum CO₂ evolved during the summer period in Washingtonstate was less than 50 percent the maximum rate shown in this tundra study. Douglas and Tedrow did not measure CO₂ production from tundra at Barrow during the late season, but they did note significant soil respiration during the period of soil thaw in June when soil temperatures were 0 - 4 C (4).

Benoit used a differential respirometer to measure soil respiration of Barrow soil between the range of -2 and 28 C and noted a Q_{10} of 1.8 over that range (1). The Q_{10} of soil respiration decreased in the temperature range of 28 to 37 C, but the Q_{10} increased in the range of -7 and -2 C. Soil respiration ceased at -7 C. Based upon the sub-zero celsius activity field values obtained in this study and the laboratory data of Benoit (1), the microflora of tundra soil appears to be physiologically capable of metabolism in the range of -7 to 0 C. If this hypothesis is correct, it provides the answer to why relatively high CO_2 values were obtained under the snow of tundra from the first snowfall until early December and also the period preceeding snow melt (8). Benoit observed that the number of bacteria in soil as measured by the aerobic spread plate technique was always at a seasonal maximum when the soil thaws in spring (1). Therefore, microorganisms not only carry on endogenous metabolism at sub-zero celsius conditions, but they may be capable of slow reproduction under these same conditions. The dynamics of soil microbiological growth has not been examined under freeze-up conditions.

Based upon theoretical grounds Vallentyne predicted that -18 C is the lower limit of active life on earth (18). Psychrophilic bacteria have been grown under laboratory conditions between 0 and -7 C (11). As the soil temperature drops below zero Celsius other inhibitory factors in soil affect microbial activity such as desiccation and increased ionic content of the water left in the unfrozen state, therefore, in tundra activity ceases before -18 C. The CO_2 flux observed during the freeze-up of tundra was consistant with the idea that microbial activity

occurs through the period of the "zero window" and continues at a reduced rate when the soil-water mixture, known on tundra, passes through the physical transition of a slurry to a slush to a solid.

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Appendix I. Daily CO₂ Evolution (mg CO₂/m²/day⁻¹) with Standard Deviations for Polygon Trough, Ridge and Basin During Freeze-up 1974 at IBP Site 4, Barrow, Ak.

| Date (1974) | Trough | SD | Ridge | SD | Basin | SD |
|-------------------|--------|-----|-------|-----|-------|-----|
| 8-30 | 2782 | 104 | 2297 | 511 | 824 | 257 |
| 8-31 | 2925 | 122 | 2334 | 371 | 1102 | 144 |
| 9-1 | 2856 | 218 | 2715 | 281 | 965 | 191 |
| 9-2 | 2729 | 225 | 1860 | 723 | 743 | 186 |
| 9-3 | 2450 | 375 | 1708 | 611 | 571 | 222 |
| 9-4 | 1867 | 165 | 1054 | 374 | 779 | 147 |
| 9-5 | 1914 | 546 | 1291 | 386 | 693 | 184 |
| 9-6 | 1893 | 447 | 1331 | 651 | 537 | 232 |
| 9-7 | 1946 | 516 | 1247 | 464 | 648 | 84 |
| 9-8 | 1722 | 351 | 943 | 229 | 725 | 85 |
| 9-9 | 1521 | 479 | 1096 | 450 | 623 | 118 |
| 9-10 | 1615 | 353 | 1422 | 702 | 617 | 139 |
| 9-11 | 1777 | 211 | 1802 | 841 | 528 | 107 |
| 9-12 | 1933 | 243 | 1261 | 442 | 596 | 55 |
| 9-13 | 1213 | 344 | 1063 | 620 | 617 | 151 |
| 9-14 | 1311 | 386 | 1118 | 508 | 613 | 132 |
| 9-15 | 1181 | 154 | 1257 | 673 | 531 | 148 |
| 9-16 | 1230 | 287 | 833 | 207 | 677 | 159 |
| 9-17 | 1316 | 305 | 1056 | 421 | 492 | 94 |
| 9-18 | 1700 | 277 | 1470 | 682 | 453 | 33 |
| 9-19 | 1593 | 100 | 1524 | 700 | 538 | 117 |
| 9-20 | 1812 | 210 | 1545 | 422 | 669 | 59 |
| 9-21 | 1619 | 378 | 1529 | 411 | 574 | 122 |
| 9-22 | 1526 | 293 | 1191 | 319 | 535 | 90 |
| 9-23 | 1169 | 119 | 1377 | 647 | 504 | 116 |
| 9-24 | 1029 | 293 | 785 | 186 | 772 | 140 |
| 9-25 | 847 | 386 | 667 | 150 | 418 | 172 |
| 9-26 | 848 | 383 | 682 | 352 | 607 | 214 |
| 9-27 | 761 | 225 | 1143 | 659 | 665 | 266 |
| 9-28 | 1253 | 399 | 814 | 342 | 627 | 375 |
| 9-29 | 1046 | 446 | 831 | 354 | 385 | 163 |
| 9-30 | 1075 | 296 | 1073 | 420 | 354 | 137 |
| 10-1 | 861 | 123 | 1527 | 187 | 428 | 263 |
| 10-2 ^a | 861 | 123 | 1527 | 187 | 428 | 263 |
| 10-3 | 695 | 246 | 393 | 75 | 207 | 77 |
| 10-4 | 644 | 158 | 435 | 146 | 300 | 70 |
| 10-5 | 578 | 97 | 330 | 0 | 265 | 87 |
| 10-6 ^a | 578 | 97 | 330 | 0 | 265 | 87 |
| 10-7 | 378 | 83 | 649 | 425 | 270 | 113 |
| 10-8 | 501 | 239 | 366 | 122 | 228 | 53 |
| 10-9 | 532 | 229 | 459 | 242 | 303 | 156 |
| 10-10 | 470 | 150 | 714 | 351 | 200 | 53 |

^a48 hr sampling due to extreme weather conditions.

Appendix I. (continued)

| Date (1974) | Trough | SD | Ridge | SD | Basin | SD |
|----------------|--------|-----|------------------|-----|------------------|-----|
| 10-11 | 519 | 86 | 714 | 278 | 307 | 194 |
| 10-12 | 689 | 269 | 466 | 67 | 366 | 200 |
| 10-13 | 304 | 45 | 414 | 172 | 310 | 174 |
| 10-14 | 311 | 134 | 350 | 211 | 233 | 113 |
| 10-15 | 200 | 48 | 377 | 121 | 185 | 138 |
| 10-16 | 311 | 176 | 214 | 97 | 192 | 88 |
| 10-17 | 230 | 110 | 256 | 157 | 209 | 119 |
| 10-18 | 203 | 91 | 182 | 92 | 178 | 58 |
| 10-19 | 131 | 65 | 182 ^a | 92 | 178 ^a | 58 |

^a48 hr sampling due to extreme weather conditions.

Appendix II. Daily Significant Subsets at the 5% Level for Polygon Trough (T), Ridge (R) and Basin (B) During Freeze-up 1974 at IBP Site 4, Barrow, Ak.

| (1974) Date | Subset 1 | Subset 2 | Subset 3 | Date | Subset 1 | Subset 2 | Subset 3 |
|----------------|-------------|-------------|-------------|-------|-------------|-------------|-------------|
| 8-30 | B | TR | | 9-25 | BRT | | |
| 8-31 | B | R | T | 9-26 | BRT | | |
| 9-1 | B | TR | | 9-27 | BRT | | |
| 9-2 | B | R | T | 9-28 | BR | TR | |
| 9-3 | B | R | T | 9-29 | BR | TR | |
| 9-4 | BR | T | | 9-30 | B | TR | |
| 9-5 | BR | TR | | 10-1 | B | T | R |
| 9-6 | B | TR | | 10-2 | B | T | R |
| 9-7 | BR | T | | 10-3 | BR | T | |
| 9-8 | BR | T | | 10-4 | BR | TR | |
| 9-9 | BR | TR | | 10-5 | BR | TR | |
| 9-10 | B | TR | | 10-6 | BR | TR | |
| 9-11 | B | TR | | 10-7 | BRT | | |
| 9-12 | B | R | T | 10-8 | BR | TR | |
| 9-13 | BRT | | | 10-9 | BRT | | |
| 9-14 | BR | TR | | 10-10 | BT | TR | |
| 9-15 | B | TR | | 10-11 | BT | TR | |
| 9-16 | BR | T | | 10-12 | BRT | | |
| 9-17 | B | TR | | 10-13 | BRT | | |
| 9-18 | B | TR | | 10-14 | BRT | | |
| 9-19 | B | TR | | 10-15 | BRT | | |
| 9-20 | B | TR | | 10-16 | BRT | | |
| 9-21 | B | TR | | 10-17 | BRT | | |
| 9-22 | B | TR | | 10-18 | BRT | | |
| 9-23 | B | TR | | 10-19 | BRT | | |
| 9-24 | BRT | | | | | | |

Appendix III. Daily CO₂ Evolution (mg CO₂/m²/day⁻¹) with Standard Deviations for Polygon Basin, Basin No Canopy² with PO₄ and Basin No Canopy Without PO₄ During Freeze-up 1974 at IBP Site 4, Barrow, Ak.

| (1974) Date | Basin | SD | Basin No canopy with PO ₄ | SD | Basin No canopy without PO ₄ | SD |
|-------------------|-------|-----|--|-----|---|-----|
| 8-30 | 824 | 257 | 576 | 57 | 642 | 126 |
| 8-31 | 1102 | 144 | | | 624 | 101 |
| 9-1 | 965 | 191 | | | 529 | 80 |
| 9-2 | 743 | 186 | 391 | 42 | 407 | 143 |
| 9-3 | 571 | 222 | 335 | 46 | 506 | 237 |
| 9-4 | 779 | 147 | | | 470 | 258 |
| 9-5 | 693 | 184 | | | 423 | 104 |
| 9-6 | 537 | 232 | 401 | 110 | 402 | 55 |
| 9-7 | 648 | 84 | 426 | 22 | 605 | 326 |
| 9-8 | 725 | 85 | | | 503 | 219 |
| 9-9 | 623 | 118 | | | 407 | 54 |
| 9-10 | 617 | 139 | 406 | 96 | 412 | 53 |
| 9-11 | 528 | 107 | 342 | 17 | 388 | 99 |
| 9-12 | 596 | 55 | | | 444 | 241 |
| 9-13 | 617 | 151 | | | 410 | 117 |
| 9-14 | 613 | 132 | 312 | 82 | 410 | 49 |
| 9-15 | 531 | 148 | 236 | 69 | 470 | 243 |
| 9-16 | 677 | 159 | | | 417 | 229 |
| 9-17 | 492 | 94 | | | 334 | 112 |
| 9-18 | 453 | 33 | 340 | 164 | 301 | 43 |
| 9-19 | 538 | 117 | 334 | 24 | 410 | 114 |
| 9-20 | 669 | 59 | | | 317 | 71 |
| 9-21 | 574 | 122 | | | 298 | 38 |
| 9-22 | 535 | 90 | 375 | 154 | 311 | 71 |
| 9-23 | 504 | 116 | 438 | 102 | 481 | 197 |
| 9-24 | 772 | 140 | | | 582 | 287 |
| 9-25 | 418 | 172 | | | 323 | 81 |
| 9-26 | 607 | 214 | 619 | 312 | 365 | 175 |
| 9-27 | 665 | 266 | 517 | 79 | 407 | 167 |
| 9-28 | 627 | 375 | | | 280 | 123 |
| 9-29 | 385 | 163 | | | 268 | 122 |
| 9-30 | 354 | 137 | 438 | 400 | 166 | 80 |
| 10-1 | 428 | 263 | 276 | 156 | 236 | 101 |
| 10-2 ^a | 428 | 263 | 276 | 156 | 236 | 101 |
| 10-3 | 207 | 77 | | | 308 | 307 |
| 10-4 | 300 | 70 | | | 316 | 150 |
| 10-5 | 265 | 87 | | | 245 | 170 |
| 10-6 ^a | 265 | 87 | | | 245 | 170 |
| 10-7 | 270 | 113 | 211 | 97 | 298 | 167 |
| 10-8 | 228 | 53 | | | 158 | 86 |
| 10-9 | 303 | 156 | | | 174 | 39 |

^a48 hr sampling due to extreme weather conditions.

Appendix III. (continued)

| (1974) Date | Basin | SD | Basin No canopy with PO ₄ | SD | Basin No canopy without PO ₄ | SD |
|--------------------|-------|-----|--|-----|---|-----|
| 10-10 | 200 | 53 | 130 | 107 | 136 | 52 |
| 10-11 | 307 | 194 | 315 | 203 | 171 | 105 |
| 10-12 | 366 | 200 | | | 257 | 158 |
| 10-13 | 310 | 174 | | | 269 | 39 |
| 10-14 | 233 | 113 | 99 | 43 | 188 | 80 |
| 10-15 | 185 | 138 | 85 | 74 | 144 | 84 |
| 10-16 | 192 | 88 | | | 181 | 83 |
| 10-17 | 209 | 119 | | | 194 | 123 |
| 10-18 | 178 | 58 | 149 | 43 | 199 | 33 |
| 10-19 ^a | 178 | 58 | 149 | 43 | 199 | 33 |

^a48 hr sampling due to extreme weather conditions.

Appendix IV. Daily Significant Subsets at the 5% Level for Polygon Basin (A), Basin No Canopy with PO₄ (B) and Basin No Canopy without PO₄ (C) During Freeze-up 1974 at IBP Site 4, Barrow, AK.

| Date (1974) | Subset 1 | Subset 2 | Subset 3 | Date | Subset 1 | Subset 2 | Subset 3 |
|----------------|-------------|-------------|-------------|-------|-------------|-------------|-------------|
| 8-30 | ABC | | | 9-25 | AC | | |
| 8-31 | A | C | | 9-26 | ABC | | |
| 9-1 | A | C | | 9-27 | ABC | | |
| 9-2 | A | BC | | 9-28 | AC | | |
| 9-3 | ABC | | | 9-29 | AC | | |
| 9-4 | A | C | | 9-30 | ABC | | |
| 9-5 | A | C | | 10-1 | ABC | | |
| 9-6 | ABC | | | 10-2 | ABC | | |
| 9-7 | ABC | | | 10-3 | AC | | |
| 9-8 | A | C | | 10-4 | AC | | |
| 9-9 | A | C | | 10-5 | AC | | |
| 9-10 | A | BC | | 10-6 | AC | | |
| 9-11 | A | BC | | 10-7 | ABC | | |
| 9-12 | AC | | | 10-8 | AC | | |
| 9-13 | A | C | | 10-9 | AC | | |
| 9-14 | A | BC | | 10-10 | ABC | | |
| 9-15 | AC | BC | | 10-11 | ABC | | |
| 9-16 | A | C | | 10-12 | AC | | |
| 9-17 | A | C | | 10-13 | AC | | |
| 9-18 | ABC | | | 10-14 | ABC | | |
| 9-19 | AC | BC | | 10-15 | ABC | | |
| 9-20 | A | C | | 10-16 | AC | | |
| 9-21 | A | C | | 10-17 | AC | | |
| 9-22 | AB | BC | | 10-18 | ABC | | |
| 9-23 | ABC | | | 10-19 | ABC | | |
| 9-24 | AC | | | | | | |

Appendix V. Daily CO₂ Evolution (mg CO₂/m²/day⁻¹) with Standard Deviations for Polygon Ridge, Ridge No Canopy with PO₄ and Ridge No Canopy without PO₄ During Freeze-up 1974 at IBP Site 4, Barrow, AK.

| Date (1974) | Ridge | SD | Ridge No canopy with PO ₄ | SD | Ridge No canopy without PO ₄ | SD |
|----------------|-------|-----|--|------|---|------|
| 8-31 | 2334 | 371 | 2139 | 708 | 2266 | 843 |
| 9-1 | 2715 | 281 | 2170 | 536 | 2147 | 791 |
| 9-4 | 1054 | 374 | 1727 | 788 | 1580 | 953 |
| 9-5 | 1291 | 386 | 934 | 260 | 1117 | 772 |
| 9-8 | 943 | 229 | 1495 | 859 | 1339 | 881 |
| 9-9 | 1096 | 450 | 820 | 213 | 903 | 653 |
| 9-12 | 1261 | 442 | 1740 | 835 | 1615 | 914 |
| 9-13 | 1063 | 620 | 825 | 292 | 721 | 271 |
| 9-16 | 833 | 207 | 1505 | 861 | 1204 | 877 |
| 9-17 | 1056 | 421 | 865 | 344 | 514 | 85 |
| 9-20 | 1545 | 422 | 1819 | 718 | 1650 | 787 |
| 9-21 | 1529 | 411 | 1145 | 253 | 1152 | 692 |
| 9-28 | 814 | 342 | 1148 | 898 | 1179 | 503 |
| 9-29 | 831 | 354 | 1041 | 628 | 1344 | 1019 |
| 10-3 | 393 | 75 | 2109 | 1044 | 1479 | 954 |
| 10-4 | 435 | 146 | 857 | 707 | 1089 | 1088 |
| 10-8 | 366 | 122 | 683 | 235 | 1225 | 552 |
| 10-9 | 459 | 242 | 542 | 252 | 646 | 633 |
| 10-12 | 466 | 67 | 509 | 274 | 1177 | 670 |
| 10-13 | 414 | 172 | 465 | 252 | 372 | 207 |
| 10-16 | 214 | 97 | 525 | 175 | 565 | 151 |
| 10-17 | 256 | 157 | 422 | 230 | 369 | 165 |

Appendix VI. Daily Significant Subsets at the 5% Level for Polygon Ridge (A), Ridge No Canopy with PO₄ (B) and Ridge No Canopy without PO₄ (C) During Freeze-up 1974 at IBP Site 4, Barrow, AK.

| Date (1974) | Subset 1 | Subset 2 | Subset 3 |
|----------------|-------------|-------------|-------------|
| 8-31 | ABC | | |
| 9-1 | ABC | | |
| 9-4 | ABC | | |
| 9-5 | ABC | | |
| 9-8 | ABC | | |
| 9-9 | ABC | | |
| 9-12 | ABC | | |
| 9-13 | ABC | | |
| 9-16 | ABC | | |
| 9-17 | ABC | BC | |
| 9-20 | ABC | | |
| 9-21 | ABC | | |
| 9-28 | ABC | | |
| 9-29 | ABC | | |
| 10-3 | AC | BC | |
| 10-4 | ABC | | |
| 10-8 | AB | BC | |
| 10-9 | ABC | | |
| 10-12 | ABC | | |
| 10-13 | ABC | | |
| 10-16 | ABC | | |
| 10-17 | ABC | | |

Appendix VII. Daily Minimum, Maximum and Mean Soil Temperatures at 5 cm Depth of Tundra During Freeze-up 1974 at IBP Site 4, Barrow, AK.

| Date (1974) | Minimum | Maximum | Mean | Date | Minimum | Maximum | Mean |
|------------------|---------|---------|------|--------------------|---------|---------|------|
| 8-29 | 5.8 | 10.6 | 9.5 | 9-28 | 1.4 | 2.0 | 1.8 |
| 9-7 ^a | 0.6 | 5.0 | 2.15 | 9-29 | 1.6 | 2.2 | 1.8 |
| 9-8 | 0.8 | 3.4 | 1.9 | 9-30 | 1.4 | 1.8 | 1.8 |
| 9-9 | 1.0 | 3.2 | 1.8 | 10-1 | 0.6 | 1.4 | 1.2 |
| 9-10 | 1.0 | 2.4 | 1.5 | 10-2 | 0.4 | 1.4 | 0.9 |
| 9-11 | 1.0 | 3.6 | 1.8 | 10-3 | -0.4 | 0.4 | -0.1 |
| 9-12 | 1.6 | 2.4 | 2.0 | 10-4 | -0.6 | 0.2 | -0.3 |
| 9-13 | 1.6 | 2.0 | 1.8 | 10-5 | -2.8 | -1.4 | -2.2 |
| 9-14 | 1.4 | 2.0 | 1.6 | 10-6 | -3.2 | -2.6 | -3.0 |
| 9-15 | 1.4 | 1.4 | 1.4 | 10-7 | -2.4 | -0.2 | -1.1 |
| 9-16 | 1.4 | 1.8 | 1.7 | 10-8 | -0.6 | 0.4 | -0.2 |
| 9-17 | 1.6 | 2.8 | 2.0 | 10-9 | -0.4 | 0.6 | 0.1 |
| 9-18 | 1.6 | 4.2 | 2.7 | 10-10 | 0.4 | 1.4 | 0.8 |
| 9-19 | 1.6 | 8.0 | 4.1 | 10-11 | -0.2 | 1.6 | 0.7 |
| 9-20 | 1.8 | 7.4 | 4.2 | 10-12 | -0.8 | -0.2 | -0.5 |
| 9-21 | 2.4 | 5.6 | 4.1 | 10-13 ^a | - | - | - |
| 9-22 | 1.0 | 2.0 | 1.5 | 10-14 | -5.2 | -4.8 | -5.0 |
| 9-23 | 0.4 | 1.0 | 0.8 | 10-15 | -5.6 | -5.2 | -5.4 |
| 9-24 | 0.4 | 1.0 | 0.6 | 10-16 | -6.6 | -5.6 | -6.0 |
| 9-25 | 0.2 | 0.6 | 0.4 | 10-17 | -5.6 | -4.2 | -4.9 |
| 9-26 | 0.2 | 0.4 | 0.4 | 10-18 | -7.4 | -5.6 | -6.5 |
| 9-27 | 0.6 | 1.8 | 1.2 | | | | |

^a recorder malfunction.

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IN SITU CARBON DIOXIDE FLUX FROM ARCTIC TUNDRA
DURING FREEZE-UP

by

Tyree Woodrow Kessler, Jr.

(ABSTRACT)

The relationship between soil temperature and CO₂ flux from undisturbed soil cores was examined during freeze-up of arctic tundra. Three habitats which dominate tundra topography, polygon trough, ridge and basin, produced significantly different amounts of CO₂ when soil temperatures were above 0 C. A significant positive correlation between soil temperatures between 10 to -7 C and CO₂ flux from each habitat was established. Substantial quantities of CO₂ were produced during freeze-up period when soil temperatures remained near 0 C for an extended period, and the CO₂ production continued at reduced levels as the soil temperature dropped below 0 C. When soil temperatures reached -7 C and the study was terminated, the CO₂ flux was reduced to a low level, but did not reach extinction. A maximum CO₂ flux of 2925 mg CO₂/m²/day from the trough habitat was observed when the soil temperature was 10 C, and the minimum CO₂ flux of 131 mg/m²/day was observed when the soil temperature was -7 C. These data are consistent with the hypothesis that soil microorganisms in arctic tundra are capable of physiological activity in the range of 0 to -7 C.